

The University of Chicago
FOUNDED BY JOHN D. ROCKEFELLER

THE ORIGIN OF THE CRANIAL GANGLIA
IN AMEIIURUS

A DISSERTATION

SUBMITTED TO THE FACULTY
OF THE
OGDEN GRADUATE SCHOOL OF SCIENCE
IN CANDIDACY FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY



BY
F. L. LANDACRE

REPRINTED FROM THE JOURNAL OF COMPARATIVE
NEUROLOGY AND PSYCHOLOGY
VOLUME 20, No. 4, 1910

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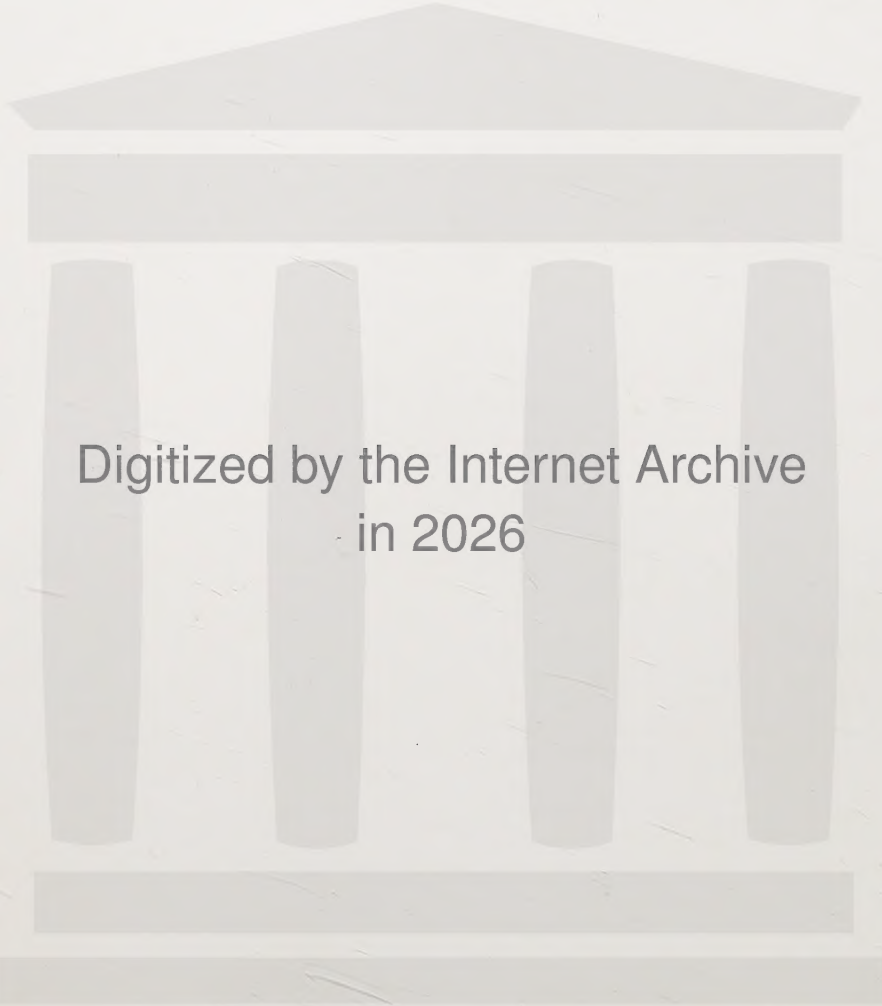
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F. L. LANDACRE

EIGHTY-EIGHT FIGURES

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INTRODUCTION

The origin and relationship of the cerebral nerves have been, since the appearance of Balfour's classical researches on the nerves of Elasmobranchs in 1876, among the most interesting and puzzling problems in vertebrate morphology. Notwith-

standing the enormous amount of labor expended on this problem, it can hardly be said that there is any general agreement among workers as to the mode of origin or fundamental relationships of the various cerebral nerves to each other.

The lack of agreement may be traced to several causes aside from the difficulty inherent in the problem. Chief among these causes must be placed the subordination of the study of the cerebral nerves to more general problems, such as the metamerism of the vertebrate head and the relation of the head to the trunk. These fundamental problems have been a source of intense interest to both morphologists and embryologists and it was only natural that the cerebral nerves should be used as a means of shedding light on them, even when the origin, composition and distribution of the nerves were not accurately known.

Owing to this method of approach, however, students of the cerebral nerves were for a long time handicapped by preconceived notions as to the relations which ought to exist between the trunks of the cerebral nerves and the various head segments. The idea of the serial homology of the cerebral nerves has been in a sense a barrier to a clear understanding of their true relationships. The chief function of the nervous system as a coördinating mechanism was lost sight of in the attempt to reduce the cerebral nerves to some fundamental type that would bring them into harmony with each other and with the spinal nerves.

Some such fundamental relationship among the cerebral nerves as that involved in the idea of serial homology probably existed in a primitive vertebrate; but the cerebral nerves of the Ichthyopsida are not most easily understood on such a basis. The fundamental needs of the organism have so modified this primitive type that it is much easier and more in accord with the facts to take some functional unit, such as a sensory system, as a basis for the analysis of the cerebral nerves.

The fundamental difficulty in the attempt to homologize the trunks of the cerebral nerves comes from the fact that they are not units but composite in nature, so that the components of which they are made up furnish the logical basis for getting at their true relationships.

The realization of this fact and its use as a working basis in the attempt to determine the relationships of the cerebral nerves is the most striking characteristic of recent work on the nervous system of the lower vertebrates. The recognition of functional units rather than serial homologies as the keynote in this work has tended to free the study of the cerebral nerves from subordination to larger problems and to call attention to the need as well as to the possibility of a more thorough knowledge of the composition of the nerves before this knowledge can be applied to such problems as the metamerism of the head or to the relation of the head to the trunk. It has also served to bridge the gap that has existed between the structural and functional conceptions of the nerves by adopting a unit that is not only structural in character but functional as well.

Such an analysis of the cerebral nerves has been possible, owing to the fact that, among other things, there are structural differences between the various components that have made it possible to follow them throughout their whole course in favorable types. The analysis has been materially strengthened of course by a clearer understanding of the various types of end organs to which the fibers are distributed peripherally as well as of the central connections in the brain and cord.

The net result of this work seems to have changed the basis for homologizing the cerebral nerves from the nerve trunks to the nerve components. These are anatomical and physiological units characterized by similarity in function, peripheral distribution and central connections; but they are not uniformly distributed throughout the various cerebral nerves even in closely related types. Nerves with the same name and the same general topographical relations may vary totally in composition. This fact makes it evident that there could be no agreement as to the homology of the cerebral nerves as long as their exact composition was unknown.

A more thorough knowledge of the components of which the cerebral nerves are made up and of the composition and position of the ganglia from which they arise opens the question as to the origin of the discrete elements of these ganglia. Are

they as distinct from each other in their mode of origin as they are in their structure and function in the adult?

Even a cursory reading of the literature on cerebral nerves shows a well defined movement away from the idea of concreteness of origin and toward that of discreteness of origin. Recently however, so far as I am aware, no attempt has been made to follow out carefully the development of the cerebral ganglia in some type in which the nerve components are known. The present paper is an attempt to fill this gap in our knowledge by tracing the various components back to their earliest recognizable stages, keeping in mind the fact that the origin of a definitive ganglionic mass of known composition and function in the adult is the end in view. The attempt to account for the fate of all embryonic cell masses, a part of which may go to form ganglia, presents a totally different problem and one with which we are unable to cope with present technical methods.

I wish to express my gratitude to Dr. C. O. Whitman for his friendly criticism and guidance during the progress of this work.

HISTORICAL SKETCH

The following brief historical account aims to give only the important advances by which our knowledge of the discreteness in origin and structure of the cranial ganglia and nerves has grown.

According to Balfour ('75), before the appearance of his work on the spinal ganglia in Elasmobranchs, it was the prevailing opinion that the ganglia were derived from the mesoblast of the vertebrae. His had in 1868 ascribed their origin to the epiblast but his work seems not to have been confirmed up to the time Balfour published. Balfour, as is well known, traced the ganglia to the cord but believed that his work diverged from that of His no less than from that of his own predecessors. Goette and Semper, writing in 1875, however, had attributed the origin of the nerves to the epiblast and Goette had extended this observation to the head. In 1882 Van Wijhe and Hoffmann, working on teleosts, confirmed Goette's work and Van Wijhe showed that the neural

crest cells fuse with the lateral ectoderm in two places. This was confirmed for amphibia in 1886 by Misses Johnson and Sheldon, who like Van Wijhe found that the dorsal fusion is connected with the lateral line.

In 1885 Froriep described in mammals, what he designated as branchial sense organs on the facialis, glossopharyngeus and vagus nerves. The epidermal thickenings which he figures and designates as branchial sense organs are undoubtedly epibranchial placodes since they lie immediately over the gill slits and there are no lateral line nerves in the mammals. Froriep, however, thinks that the resemblance of these anlagen to those of the lateral line anlagen places them in that group of nerves. He further finds that the evidence for the addition of cells from the placode to the ganglia in these nerves is slight, since only in the earlier stages are the boundaries between the two structures indistinct.

Beard ('85, '87, '88) described primitive branchial sense organs in elasmobranchs, teleosts, amphibia, reptiles and birds and also stated that the epidermal thickening contributed cells to the ganglia derived from the neural crest. Beard rejected the term lateral line organ because the lateral lines originate in the head and substituted therefor the term branchial sense organ, and he seems always to have had in mind the lateral line organs of the head when he speaks of branchial sense organs; at least he confuses the dorso-lateral and the ventro-lateral placodes and, as von Kupffer ('91) intimates, it is impossible to tell which he is discussing at times. He figures and mentions, however, two points of contact of the neural crest ganglia with the skin.

Beard ('88, p. 882) refers to the fusion of the neural crest with the epiblast at the level of the notochord, and just above the gill cleft in the same paragraph, apparently not distinguishing between them, although in the same paper he criticizes Onodi for not having seen the second fusion of the ganglion anlage with the epiblast. It seems a safe conclusion from Beard's papers that he took all fusions of the neural crest to be concerned in the formation of the lateral nerves.

In discussing the origin of the neural crest portion of the ganglia Beard ('88) insists that the origin of the spinal ganglia from the

Zwischenstrang as described by His is not correct but that in all cases he finds the ganglion arising from a mass of cells derived from the epiblast at the point of the entering angle between epiblast and cord and that the Zwischenstrang takes no part in its formation and is present after the ganglion has detached itself from the epiblast and that the ganglion anlage can always be detected before the closing in of the medullary plates. Beard failed, however, as his predecessors had failed, to distinguish between the dorso-lateral placodes and the early stages of the adult lateral line organs. Under the term branchial sense organs he may have been describing either lateral line organs in the head, or dorso-lateral placodes which may give rise to ganglion cells. Von Kupffer, working on *Petromyzon*, in 1891 made a sharp distinction on the one hand between dorso-lateral placodes or those placodes concerned in the origin of the lateral line and lying at the level of the notochord, and on the other hand the epibranchial placodes which arise just over the gill slits. He also states that the epibranchial ganglia are concerned in the origin of the branchial nerves, so that one may infer from his work that there were separate origins for what we now designate as lateralis and visceral sensory nerves.

Miss Platt ('95) showed that in *Necturus* the lateral ectoderm gives rise not only to the lateral line ganglia and nerves which appear in three primitive longitudinal ridges, but also to mesectoderm, cells proliferated from the lateral ectoderm and from the neural crest and assuming the position and characteristics of mesoderm. Miss Platt seems first to have made a distinction between the earliest thickening of the lateral epidermis, *i.e.*, the dorso-lateral and epibranchial placodes, and the early stages of the lateral line organs. These seem to have been confused by previous workers. She says (p. 500) that "the large dorso-lateral and epibranchial ganglia are formed from cells that split off *en masse* leaving the ectoderm external to them for the time thin. A sensory ridge may appear later in the exact place where the ganglion arose, as happens in the supra-orbital line, or sense organs may form at either side of the ganglionic anlage, as in the vagus region." She calls attention (p. 497) to the fact that the growing point of

the dorso-lateral placode may simulate very closely a lateral line organ (fig. 5), but that it does not give rise directly to these organs since this growing point is found in segments where later there are no lateral line organs.

Miss Platt's work marks in a way the culmination of the work begun by Balfour in 1876. A more thorough analysis of the cerebral nerves of the adult was needed before the full significance of the dorso-lateral and epibranchial placodes could be determined. While she seems to place the dorso-lateral and epibranchial placodes in the same category, the determination that not all cells proliferated from the neural crest and epidermis go to form ganglia and that the dorso-lateral placodes do not in some cases give rise directly to sense organs, but that these appear later, mark distinct advances in our knowledge of the origin of structures derived from the epidermis. Much confusion has arisen apparently from ignorance of these facts.

Locating a specific ganglion of known composition in the adult and then tracing it to its origin would have prevented errors that have arisen unavoidably from pursuing the opposite course and finding a segmental ganglion and nerve for every area in which cells are being proliferated from the neural crest and ectoderm. As a general conclusion from her work, she thinks that the root of a sensory nerve is no index to the segmental value of that nerve, the position of the nerve root being in a great measure the expression of the coördinate relations which the central nervous system serves. Miss Platt emphasizes another point of the greatest importance; it is in connection with the distinction between definitive ganglion cells and nerve fibres on the one hand, and the anlagen from which these come on the other. Just as not all cells derived from the ectoderm go to form ganglia and nerves, so not all cells grouped about ganglia and the growing points of nerves are concerned directly in the nervous functions of the nerves and ganglia.

The appearance of Strong's paper in 1895, and more particularly of Herrick's in 1899, mark as it appears to the writer, a turning point in the study of the cerebral nerves. Evidently no homology of the cerebral nerves can be established without an exact knowl-

edge of the central ending, ganglionic relations, and peripheral distribution of the various components of these nerves. Confusing acustico-lateralis ganglia with communis or visceral ganglia or failing to distinguish between perfectly discrete regions in the brain leads only to confusion. The fact that in many types a difference in size of fibres, in addition to the characteristics mentioned above is present, has made possible the determination of the exact composition of the trunks of the cranial nerves and has made unnecessary the almost interminable and confusing discussions of their homologies. The determination by Herrick ('99) that there are in the Vth, VIIth, VIIIth, IXth, and Xth nerves of Ichthyopsida three, and apparently only three, chief groups of sensory components and the exact definition and description of these components and their ganglia marks in a general way the advance in our knowledge of cranial nerves since Strong's paper appeared.

The three components mentioned above are, first, the general cutaneous, characterized by ending in the brain in the spinal fifth tract, by having ganglia (in Menidia) in the Vth and Xth nerves situated intracranially, by having medium sized fibres and by being distributed peripherally to the skin as free nerve endings. Second, the acustico-lateralis, or special cutaneous, characterized by ending in the brain in the tuberculum acusticum, by having ganglia in the VIIth, VIIIth, and Xth nerves, by having large fibres and by being distributed to the ear and lateral line organs only. Third, the communis or visceral sensory system characterized by ending in the brain in the nucleus of the fasciculus solitarius or its equivalent in the vagal, glossopharyngeal, and facial lobes, by having ganglia in the VIIth, IXth and Xth nerves, by having small sized fibres and by ending peripherally in taste buds wherever found, and general mucous surfaces. While this paradigm holds for teleosts generally, the irregularity with which some of these components are distributed in the various cerebral trunks makes it clear why there was so much confusion and disagreement in the earlier attempts to determine the homologies of these trunks.

A comparison of Koltzoff's excellent paper ('02) on the embryology of *Petromyzon* with the work of Johnston ('05*b*) on the nerve components of the same type will serve to introduce the point of view from which the author has worked the early stages of the ganglia in *Ameiurus*. Koltzoff does not list a single nerve component paper in his bibliography and was in fact working primarily on the segmentation of the head, and only incidentally on the origin of the ganglia. The results of these two papers are summarized in the following diagram:

TABLE I

Summarizing the results of Koltzoff's work on the development of the ganglia in Petromyzon, and of Johnston's on the adult structure of the same form

		PROF. OR TRIG. I. V	TRIG. OR TRIG. II. V	VII	VIII	IX	X
Koltzoff (Derivative)	Neu. Crest..	Neu. crest	Neu. crest	Neu. crest	Neu. crest	Neu. crest	Neu. crest Segmental
	D. L. Plac...	D.L. Plac.	D.L. Plac.	D.L. Plac.	D.L. Plac.	D.L. Plac.	D.L. Plac.
	Ep. Plac.....			Ep. Plac.		Ep. Plac.	Ep. Plac. Segmental
Johnston (Component)	General Cutaneous	Prof. N. and Gan..	Trig. N. and Gan..	Gen. Cut. VII		Gen. Cut. IX	Gen. Cut. X. Segmental
	Acustico- Lateralis ...	Lateralis Prof.	Lateralis Trig.	Lateralis VII	Auditory.	Lateralis IX	Lat. X. Not Segmental
	Communis or Visceral.			Com. VII.		Com. IX.	Com. X. Segmental

It will be seen at a glance that every nerve into whose ganglion cells derived from the epibranchial placode enter contains in the adult visceral fibres; every nerve to whose ganglion the dorso-

lateral placodes contribute cells contains acustico-lateralis fibres in the adult; and, finally, every nerve, except the eighth, to whose ganglion the neural crest contributes cells contains in the adult general cutaneous fibres.

If it were not for the single exception in the case of the VIIIth nerve, a very natural conclusion from this comparison would be that the epibranchial placodes gave rise to visceral ganglia, the dorso-lateral placodes to acustico-lateralis ganglia and the neural crest to general cutaneous ganglia. The error in this conclusion arises from the assumption that the epibranchial and dorso-lateral placodes give rise to all of the ganglia into which they enter. This may occur in some cases but certainly does not in all. There is a very general agreement among workers on the origin of the cerebral ganglia that the neural crest cells fuse with cells derived from either the dorso-lateral placodes or the epibranchial placodes or both, so that the assumption that these placodes give rise to all of the ganglia into which they enter is not only unwarranted but contrary to evidence presented in a large number of cases. If neural crest cells enter into the auditory ganglion of *Petromyzon*, which is the most specialized of all the acustico-lateralis ganglia, it would not be surprising if they should enter into the less specialized ganglia, such as those of the VIIth nerve. An examination of the literature on the composition of the auditory ganglion shows a great deal of diversity of opinion as to the presence of the neural crest in the region of the auditory vesicle. Johnston ('06) states that it is absent and Rabl ('92) and Hoffmann ('94) both take the same position. On the other hand, Beard ('88), Van Wijhe ('82), von Kupffer ('94), Platt ('95) and Neal ('97) hold that it is present. There seems little doubt that it is present in some types in the earlier stages at least. It does not follow from this fact that neural crest cells enter into the auditory ganglion. Dohrn ('90) holds that the neural crest is at first continuous between the acustico-facialis and the glossopharyngeus, but later disappears, that it is sometimes present on both sides and sometimes only on one side and that the masses of cells which he sometimes finds are to be interpreted as remnants of the former connections of preauditory and postauditory neural crest. The fact that there are general

cutaneous fibres in the VIIth in *Petromyzon*, that the crest is at first continuous but apparently not so later, and that when the VIIth and IXth contain general cutaneous fibres they also contain neural crest cells seem to the writer to minimize the discrepancy between Kolzoff's and Johnston's work, since these cells may enter into the VIIth and IXth in *Petromyzon*. The matter is complicated by the fact that neural crest cells of the VIIth lie between the anterior portion of the auditory vesicle and the neural tube and come into contact with the vesicle at or near the place where the cells of the auditory ganglion are proliferated from the vesicle so that the relations are confused and it is difficult to be certain of the exact conditions. Leaving out of consideration the VIIIth ganglion, we can infer that the general cutaneous ganglia come exclusively from the neural crest, while the acustico-lateralis and visceral ganglia come in part from the dorso-lateral and epi-branchial placodes respectively but may contain neural crest cells in some cases.

Without anticipating the conclusions drawn from a study of *Ameiurus*, it may be well to call attention to two facts: first, the acustico-lateralis system of nerves and ganglia is usually treated as a special cutaneous system on account of the fact that the tuberculum acusticum which is the acustico-lateralis center in the medulla oblongata is a specialized portion of the general cutaneous center of the spinal cord extending into the medulla oblongata. The close relationship of the general cutaneous and acustico-lateralis systems is thus based on good anatomical evidence. Second, the communis or visceral system is really double in character; it consists of a general visceral portion which supplies general mucous surfaces, and it also contains a special visceral or gustatory portion whose fibres end peripherally in taste buds, so that the presence of neural crest cells in the acustico-lateralis and visceral ganglia might be explained in the first case on the basis of the close relationship between the general cutaneous and the acustico-lateralis systems of nerves and ganglia and in the second case on the basis of the double composition of the communis or visceral system.

The determination of the relation of neural crest cells to those

cells derived from the dorso-lateral and epibranchial placodes was one of the chief objects in taking up the study of *Ameiurus*. Unexpected difficulties were met, owing to the fact that *Ameiurus* has no well defined neural crest in the head such as is found in other types, so that my conclusions are based on the assumption that there are in *Ameiurus* cells which correspond to the neural crest of other types. Aside from this peculiarity, it has proven to be an exceptionally favorable type. The epibranchial placodes are large and easily followed and the epibranchial ganglion of the IXth nerve seems to be a pure placodal ganglion, a fact which enables us to come to a definite conclusion in regard to the relation of the neural crest cells to those derived from the placode. It seems to be necessary to determine this point definitely before we can come to any satisfactory conclusion as to the relation of the spinal and cerebral ganglia to each other. The acustico-lateralis and gustatory nerves are peculiar to the head but the general visceral and the general cutaneous are not, being found in the trunk. The problem of the relation of spinal and cerebral nerves becomes largely a question as to how the general visceral and general cutaneous nerves are related in origin to the special visceral and special cutaneous nerves in the head. Aside from the fact that it was necessary to choose some type in which the nerve components are known, the chief reason for taking *Ameiurus* lies in the enormous size of the gustatory system of sense organs and nerves. The taste buds are distributed over practically the whole body surface as well as in the mouth, pharynx and œsophagus, and gustatory fibres are found in ten out of twelve of the chief nerves arising from the trigemino-facial ganglia. A type with such an enormously hypertrophied gustatory system seemed likely to furnish a good basis for determining the exact mode of origin of the special visceral ganglia and nerves.

A summary of the cranial ganglia of *Ameiurus* as given by Herrick ('01) is shown in the following diagram:

TABLE II

Showing the components of the Vth to Xth ganglia in Ameiurus; compiled from Herrick's ('01) description. The presence of any component is indicated by "pres," or by the name of the ganglion. The jugular and lateralis Xth are placed over the third and fourth epibranchial ganglia of the Xth not to indicate their segmental position but because this is their relative position.

	V	VII	VIII	IX	X	X	X	X
Gen. Cut....	Gass.							Jugular
Acus. Lat...		Lat. VII.	Pres.	Pres.				Pres.
Communis ..		Pres.		Pres.	Pres.	Pres.	Pres.	Pres.

This table is slightly different from Herrick's description. There is a lateralis ganglion in the region of the IXth nerve which he seems to attribute ('01, p. 208) morphologically to the Xth, although it is associated with the root of the IXth. I find it to be entirely distinct in origin from the Xth nerve and have placed it in the diagram with the IXth. The general cutaneous ganglia are found in the Vth and Xth nerves. The acustico-lateralis ganglia are found in the VIIth, where there are two divisions, the dorso-lateral and the ventro-mesial; and in the VIIIth, IXth, and Xth. The visceral ganglia are found in the VIIth, IXth and in the four branchial ganglia of the Xth. The jugular or general cutaneous Xth and the lateralis Xth are placed in the diagram over the last epibranchial ganglion of the Xth, not to indicate their segmental position but because they form the posterior portion of the vagus ganglion. Attention will be called later in the body of the paper to the fact that this table makes no distinction between the general and special visceral ganglia, both being catalogued as the visceral sensory or communis system, although Herrick distinguishes the two groups functionally and further distinguishes the two types of fibres structurally.

MATERIAL AND METHOD

In a type which develops so rapidly as *Ameiurus*, there being only five days between fertilization and hatching, the age seems to be a better way to designate a series than the body length. Series must be taken at close intervals and, while individuals of a given age may not vary by an appreciable amount in length, there are frequently found in the same series quite perceptible variations in the degree of differentiation of the ganglia and sense organs, so that while the age is not an absolutely accurate method of designating a series since the growth varies with temperature, I have used this on account of the difficulty of separating embryos by their length.

As to method, I have followed consistently the plan of locating definite ganglia in older series after they were well defined and tracing these back to the earliest recognizable stages. This plan seems to be absolutely necessary, since only in a few cases do the definitive ganglia use all of the material from which they are formed and in some cases, particularly the general cutaneous ganglia, only a very small portion of the mass from which the ganglion is formed finally enters into the composition of the ganglion. Some confusion seems to have arisen, especially in the earlier work on nerves and ganglia, from taking it for granted that all of the material from which a ganglion forms enters into a ganglion.

The material on which this work was done is in part, the same as that used in a former paper by the author (Landacre, '07) and consists of series of *Ameiurus melas* of which the absolute age is known since the process of oviposition was observed; and in part, particularly the early stages, the work was done on a large number of graded series of *Ameiurus nebulosus* of which the relative age was known but the absolute age was not known. The series of *Ameiurus melas* are indicated by their ages. Of the *nebulosus* material nine stages were used of which the last two series, VIII and IX, are quite similar to each other and correspond closely to the forty-nine hour series of *A. melas*. Series I seems to be about twenty-four hours old compared with a similar stage of *A. melas*. The remaining series II to VII inclusive are all younger

than the youngest of the *A. melas* series, which was forty-nine hours old. In the following brief characterization of the stages the optic cup, the optic lens, and the auditory vesicle are used chiefly as a means of separating them in addition to the more minute differences to which attention is called in the body of the paper.

Stage I. An early stage (24 hours?) of *A. nebulosus* in which the blastoderm is nearly flat, the neural keel being elevated slightly above the yolk at the anterior end only. The blastoderm has not extended sufficiently far posteriorly and ventrally to be cut on the ventral side of the yolk sac at the posterior end of the embryo. Fig. 1 was drawn from this stage.

Stage II. Optic vesicle present, but solid. Nuclei of cells in optic vesicle uniformly distributed with no indication of the peripheral arrangement of the nuclei which precedes the formation of a cavity. Nuclei of auditory vesicle irregularly arranged with no indication of a cavity. The auditory vesicle can be located only by comparison with an older series. Lateral mass not broken down into mesectoderm at any point. Figs. 2 and 3 are drawn from this stage.

Stage III. Optic vesicle solid but with nuclei of cells uniformly arranged around the periphery of the vesicle preparatory to the formation of the optic cup. Auditory vesicle with its cells elongated and the nuclei arranged around the periphery. The lateral walls of the cup not in contact, the future cavity of the cup filled with spherical cells. The solid lateral mass of the preceding stage changed into a loose mass of tissue in the region of the Gasserian ganglion, particularly just anterior and posterior to this point. The pre- and postauditory placodes are present. Figs. 4, 5, 6, 7, 8, 9 were drawn from this stage.

Stage IV. Optic vesicle with slight cavity. Epidermis not thickened preparatory to the formation of a lens. Auditory vesicle with a slight cavity and the lateral walls of the vesicle in contact. Preauditory placode just detached from the auditory vesicle. Postauditory placode still in contact with the auditory vesicle. Gasserian and geniculate ganglia not sufficiently well defined to determine approximately their boundaries. Hyoid gill pocket

not yet in contact with the epidermis. Figs. 14, 15, 16, 44, 45, 46 were drawn from this stage.

Stage V. Optic vesicle and optic stalk completely open. Lens indicated by slight thickening of the epidermis. Auditory vesicle with well defined cavity and the proliferation of cells from the vesicle to form the ganglion beginning. Gasserian and geniculate ganglia distinguishable from the loose lateral mass cells surrounding them, although their boundaries cannot be definitely determined. Hyoid gill pocket in contact with the epidermis. First stage in the proliferation of cells from the auditory vesicle to form the lateralis IX ganglion. Hyoid gill pocket in contact with the epidermis. Figs. 10, 11, 13, 17, 18 and 63 were drawn from this stage.

Stage VI. Lens thickening well defined but changing gradually at the borders into epidermis, *i.e.*, not sufficiently thick to have its borders well defined. First epibranchial placode appears. Hyoid gill pocket still in contact with the epidermis. Figs. 19, 20, 21, 22, 23, 24 were drawn from this stage.

Stage VII. Lens constricted sharply at its borders preparatory to its detachment from the epidermis. Nuclei of cells in lens not yet located in the periphery of the cells. First epibranchial placode is proliferating cells into the mesoderm to form the first epibranchial ganglion but the ganglion is still in contact with the epidermis. The jugular ganglion of the X can be located. The lateralis X ganglion is in process of being proliferated from the postauditory placode. Hyoid gill pocket still in contact with the epidermis. Figs. 12, 25, 26, 27, 28, 29, 30, 40, 41, 42, 43, 47, 48, 49, 50, 51 were drawn from this series.

Stages VIII—IX correspond closely to a forty-nine hour embryo of *Ameiurus melas* being possibly slightly younger. There seems to be no well defined distinctions between stages VIII—IX or between these and *A. melas* forty-nine hours. The three figures drawn from these two series could have been taken from *A. melas*. Fig. 61 was drawn from Stage VIII and figs. 52, 62 from Stage IX.

All sections were cut 7μ thick and it will be convenient to express the spatial relations of structures in sections.

THE DIFFERENTIATION OF THE NEURAL PLATE

Ameiurus presents a rather striking difference from the descriptions usually given of the formation of the neural cord in its relation to the origin of the neural crest and dorso-lateral placodes.

Balfour ('75) described the neural crest as growing out of the neural cord but seems not to have worked stages sufficiently early to determine its exact mode of origin. Marshall ('77) gives substantially the same description of its origin. Beard ('88), however, describes it as arising in elasmobranchs, teleosts, amphibians, reptiles and birds as a thickening of the epidermis, lying lateral to the neural plate and always distinguishable from that structure before the neural tube is formed. There is substantial agreement among all the earlier descriptions of the cerebral ganglia in attributing to the neural crest a definite structure related more or less closely to the dorsal portion of the neural plate as it folds off to form the neural cord (Harrison '01, text-figs. 1-5). Few authors, so far as I am aware, have found any close relation between the neural crest and dorso-lateral placodes in their earliest stages. The neural crest ganglion is almost always described as growing down ventrally from its point of origin and coming into contact with the epidermis at the point of origin of the dorso-lateral placode on a level with the notochord. Wilson and Mattocks ('97, p. 659) do, however, describe the dorso-lateral placode of the salmon as arising not by a thickening of the epidermis but by the thinning out of the neural shield which leaves the placode isolated, lying in a lateral position. In the salmon the placode is at first located in the lateral portion of the neural shield just as in Ameiurus.

The early stages of Ameiurus differ from the usual descriptions in that the neural crest and dorso-lateral placodes are not differentiated from each other at first but appear as a large lateral thickening lying on either side of the neural plate. This I have designated as the *lateral mass* (fig. A.) It doubtless contains regions comparable to the neural crest and certainly to the dorso-lateral placodes of other authors; but since these are not recognizable in the early stages and in fact the neural crest is never recognizable

as a structure distinct from the lateral mass, and since the lateral mass contains much material that does not go to form ganglia before undergoing differentiation and has a definite structure and position of its own, it seems better to characterize it as indicated above.

The lateral mass in an early stage in which the neural plate is still nearly flat has the appearance indicated in fig. 1. In Stage

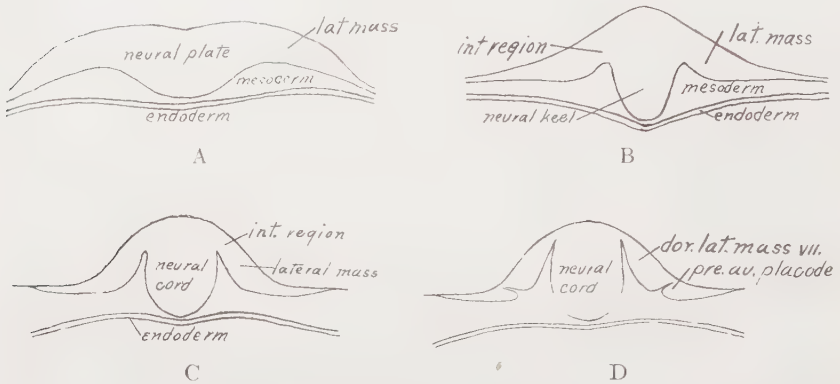


FIG. A. A camera tracing of the blastoderm corresponding to fig. 1, showing the broad, flat neural plate.

FIG. B. A camera tracing corresponding to fig. 3, showing the position of the lateral mass and of the intermediate region.

FIG. C. A camera tracing four sections anterior to fig. 9, showing the relation of the lateral mass to the neural cord.

FIG. D. A camera tracing corresponding to fig. 9, showing the relation of the preauditory placode to the dorso-lateral mass. Posterior to this point of a few sections, the auditory vesicle occupies the position of the preauditory placode and dorso-lateral mass.

II (fig. B), it is separated from the neural keel by a thinner region which I shall designate as the intermediate region to distinguish it from the lateral mass. This thickening extends throughout the whole length of the head and into the cord region. The lateral mass does not become incorporated into the neural cord which forms from the thick central mass, or neural keel, lying between the intermediate regions on either side.

As the neural keel deepens and assumes the form of a cord (fig. C), and as the blastoderm rises on the yolk and assumes a rounded form, the lateral cell masses are brought gradually into a lateral position, still retaining their connection with the dorsal half of the cord by an intermediate slightly constricted area.

In an embryo in which the optic vesicle has reached a stage in which the future optic cup is slightly larger than the stalk (Stage II), this lateral thickening begins some five or six sections posterior to the stalk and extends from this point back beyond the region in which the Xth ganglion is later formed, more than one hundred sections. Posterior to this point where the keel is forming in the region of the spinal cord it gradually becomes reduced in size as the keel becomes shallower. Throughout this whole region the lateral cell mass has a structure quite uniform at first, varying only in shape, being somewhat thicker and more closely applied to the sides of the brain in the anterior region (fig. 2), and somewhat thinner and more dorsally attached to the cord in the posterior region, particularly posterior to the position in which the auditory vesicle develops.

Six sections posterior to the optic vesicle (fig. 2), the lateral mass is applied to the dorsal half of the cord and is homogeneous in structure. This section lies in the region anterior to that in which the Gasserian ganglion later appears. In the region in which the Gasserian ganglion forms and posterior to it (fig. 3), the lateral mass is broader and thinner and the attachment to the neural cord is less extensive. This condition of the lateral mass persists throughout the region in which the Gasserian ganglion forms and back of this until we come to the region just anterior (fig. 4) and just posterior (fig. 5) to the auditory vesicle, where, in a slightly older embryo (Stage III), there is soon noticeable a slight differentiation of the lateral mass into a thicker dorsal portion, the dorso-lateral mass (*D. L. M.*, figs. 4 and 5), connected with the cord by the intermediate region, and a ventral mass (*Pre. Pl.*, fig. 4, *Post. Pl.*, 5) slightly separated from this dorsal mass on its mesial border by a constriction. This ventrally differentiated mass, or dorso-lateral placode (*pre. au. placode*, fig. D) is present throughout the whole auditory region (fig. 6),

and extends somewhat anterior and posterior to the auditory region, where it becomes merged completely with the dorso-lateral mass to form the lateral mass. Posterior to the auditory vesicle, in the region of the IXth nerve, it presents the appearance shown in fig. 5. This ventrally differentiated mass shown in figs. 4 (*Pre. Pl.*), 5 (*Post. Pl.*) and 6 (*Au. Ves.*) develops later into the auditory vesicle and the pre- and postauditory placodes (dorso-lateral placodes).

The fate of the lateral mass, as a whole, varies in different regions of the head. In the regions between the optic stalk and the Gasserian ganglion it becomes converted entirely into mesectoderm. Fig. 7 is taken from an embryo slightly older (Stage III) than that from which figs. 2 and 3 were taken, and is identical in position with fig. 2, with which it should be compared. The lateral mass is here free from the cord on its mesial border nearly to the dorsal surface of the cord; while on its lateral border it is free from the epidermis up to about the same level. The ventral two-thirds of the mass is converted into a rather loose mass of mesectoderm in which the cell boundaries are indefinite and in which there are numerous intercellular spaces.

The later history of this mass shows that it is converted completely into a very loose mass of mesectoderm with large intercellular spaces and with faint cell boundaries, but with well defined nuclei. I have detected during this change of the lateral mass into mesectoderm no mitotic figures in any of my sections. Posterior to the region in which the Gasserian ganglion forms and between that ganglion and the lateralis VIIth the lateral mass is converted chiefly into mesectoderm, except its ventral border which represents the forward extension of the primordium of the auditory vesicle, or the preauditory placode. Fig. 8 from the same embryo is taken through the region in which the Gasserian ganglion forms. The lateral mass is here detached from the cord mesially, except at its dorsal border, but it is attached to the epidermis throughout its whole length. The dorsal and particularly the dorso-mesial portion of the solid lateral mass is beginning to be converted into a looser cell mass. Fig. 9 is taken just anterior to the auditory vesicle in the position in which the lateralis VIIth ganglion will

appear. The dorsal portion of the lateral mass which is still quite solid and has definite cell walls is later converted into the lateralis VIIth ganglion and possibly in part into the anterior portion of the auditory ganglion. The ventral portion of the lateral mass (fig. 9, *Pre. Pl.*) is slightly differentiated from the dorsal and represents the preauditory placode. As one reads back in the same series this preauditory placode becomes larger (fig. 4) and the dorsal portion of the lateral cell mass smaller until the auditory vesicle is reached (fig. 6.) The change in size of the preauditory placode is almost imperceptible. It extends farther and farther dorsally until the condition of fig. 4 is reached. The auditory vesicle here has not yet incorporated all the lateral cell mass; at least all the cells of the lateral mass have not yet assumed the radial form with distally arranged nuclei which is so characteristic of the auditory vesicle.

The future lateralis VIIth ganglion is at this time quite large in front where it lies dorsal to the preauditory placode, while posteriorly it becomes smaller and assumes a dorsal and mesial position with reference to the placode. It does not extend posteriorly beyond the anterior end of the vesicle. In the region of the vesicle the whole lateral cell mass is converted into the auditory vesicle.

From this lateral cell mass are differentiated directly, first the mesectoderm lying immediately anterior and posterior to the Gasserian ganglion and posterior to the auditory vesicle. Secondly it gives rise to the Gasserian ganglion and posterior to the ear gives rise to the jugular ganglion. It also gives rise to a large part of the geniculate ganglion, excepting of course the placodal portions, and to the greater portion of the visceral ganglion of the Xth; all of it, in fact, except those portions derived from the third, fourth, fifth and sixth epibranchial placodes. In contrast with these structures which are derived primarily from the lateral mass, we have the VIIIth ganglion and the lateralis IXth which come largely, if not exclusively, from the auditory vesicle, and the lateralis Xth which comes exclusively from the postauditory placode. These may be considered as coming secondarily from the lateral mass, the auditory vesicle and postauditory placode representing the primary derivatives from this structure.

THE DIFFERENTIATION OF THE GASSERIAN GANGLION

As mentioned above, the lateral mass has at first a perfectly homogeneous structure from the region just behind the optic stalk throughout the whole length of the head.

At the time when the auditory vesicle first becomes recognizable the lateral mass anterior to the vesicle is characterized by the presence of intercellular spaces and the partial detachment of the mass from the neural canal and epidermis (fig. 7). At this stage the Gasserian ganglion is not recognizable. It becomes recognizable first by the thinning out of the mesectoderm anterior and posterior to it rather than by any change in the region of the ganglion. While the whole region from the optic stalk to the auditory vesicle is in a condition much like that represented in fig. 7, the Gasserian ganglion cannot be located.

A little later, however, when the mesectoderm has become somewhat thinner the Gasserian ganglion can be located as a somewhat condensed mass of cells extending from the region of the thirty-third section back of the optic stalk to a point just posterior to the endodermic evagination of the hyoid gill cleft. When first recognizable it occupies an area of about 12 to 15 sections and does not lie exactly parallel with the long axis of the body, its anterior end being somewhat more ventrally situated than its posterior, which lies above the level of the middle of the neural canal. There is nothing resembling a root at this stage. The whole of the posterior end of the ganglion is somewhat nearer the cord than the epidermis, but neither the root nor the trunk of the nerves from this ganglion appear for some hours. Anteriorly, as well as posteriorly, the ganglionic mass passes gradually into mesectoderm. The anterior portion of the Gasserian ganglion comes quite close to the ectoderm but there is no epibranchial placode formed in connection with this ganglion. The contact where it occurs is to be interpreted as a failure of the lateral mass to separate completely from the epidermis. The same is true of the lateral portions of the ganglionic mass. Fig. 10 (Stage V) is taken through the posterior third of the ganglion just over the hyoid gill pocket and shows the characteristic indefinite outline of the ganglionic mass shortly after it can be first recognized.

Its general shape is, in transverse section, at this time circular except at its anterior end where it is elongated dorso-ventrally and lies quite close to the epidermis. The denser appearance of the cytoplasm, with indefinite cell boundaries, is characteristic of nearly all the early ganglionic masses in *Ameiurus*. The later history of this ganglion is quite easy to follow. It becomes more definite in outline with cleaner borders and is quite distinct from any other ganglionic masses and cannot be confused with them. While in the early stages the posterior end of the Gasserian ganglion overlies that portion of the lateral mass from which the geniculate ganglion is derived, they are not in contact until about the 86th hour in *A. melas* (fig. 83). For a long time after the eighty-sixth hour, while the two ganglia are in contact, their outlines are quite distinct. Preceding this stage they are not even in contact with each other. The fibrillated root of the Gasserian ganglion appears at its posterior end where the ganglionic mass lies nearest the brain as described above, and can first be detected in an embryo of 75 hours (*A. melas*).

The development of this ganglion from the lateral mass is a very definite feature of the embryology of *Ameiurus*. There can be no doubt that it does not use all of the lateral mass in its formation and that it does not come from a neural crest as that term is generally used, although some portion of the lateral mass may be homologous with the neural crest of other types. The origin of structures which in other types come from the neural crest, and of dorso-lateral placodes from a common primordium in *Ameiurus* seems to be due to the failure of these structures to differentiate in the early stages of the lateral mass, and if it were not for the fact that so much of the lateral mass becomes converted into mesectoderm one might speak of the neural crest region of the lateral mass; but in no region is all of the lateral mass converted into a ganglion and since the specific structures derived from the lateral mass are ganglia, mesectoderm, auditory vesicle and placodes, it would only introduce confusion into the description to refer to specific portions of the lateral mass as neural crest, although in other types some of these structures are known to come from the neural crest.

THE ORIGIN OF THE LATERALIS VII GANGLIA

The origin of the lateralis VIIth ganglion resembles closely the origin of the Gasserian with the exception that the lateral mass (figs. 4 and 9, Stage III) giving rise to the lateralis VIIth never in my series breaks down so completely into a loose mass of cells as does the Gasserian. There is no break in continuity between the lateral mass cells and the ganglion. Posterior to the hyoid gill cleft, for some distance, the greater portion of the lateral mass breaks down into mesectoderm, between Stages III and V, and it is difficult to assign any definite boundary to the anterior end of the lateralis VIIth ganglion at first. Its anterior end, as in the case of the Gasserian, is situated more ventrally than the posterior end and comes into contact with the mesoderm of the mandibular arch anterior to the middle region of the arch. The anterior portion of this lateral mass later forms part of the geniculate ganglion of the VIIth nerve, but at this time the anterior limit cannot be outlined, not, in fact, until the placodal portion of the VIIth is detached from the epidermis, which is some hours later (A. nebulosus, Stage VIII). The whole ganglionic mass has an upward and backward trend, finally coming into contact with the auditory vesicle on its anterior, mesial and ventral walls. The whole ganglionic mass of the lateralis VIIth is quite homogeneous in structure, and shows no evidence of separating into the two ganglionic masses, the dorso-lateral and ventro-mesial, of which it is later composed. Its anterior boundary when it can be determined is not overlapped by the Gasserian ganglion but is overlapped by its root. Its posterior end, just where it comes into contact with the vesicle, is more closely applied to the neural tube than to the epidermis. The fibrillated root appears later at the posterior end, where it is in contact with the middle region of the cord.

Fig. 11, from the same embryo as that from which fig. 10 was taken, lies four sections anterior to the auditory vesicle. The lateralis VIIth ganglion shows the same irregular boundaries that characterized the Gasserian ganglion and is surrounded on all sides, except that next to the epidermis, by loose mesectoderm

in which cell walls are indistinguishable. The cell boundaries are still recognizable in the ganglion, however, showing its continuity with the lateral cell mass (see fig. 9). During all the earlier stages of this ganglionic mass it is impossible to locate definitely either its anterior or posterior limits. Its posterior end is in contact with the anterior end of the auditory vesicle at first and for some time also with the auditory ganglion, while its anterior end as mentioned above is in contact, if not continuous, with the posterior end of the geniculate ganglion. It is not until about the eighty-sixth hour that the boundaries of the two portions of the lateralis VIIth ganglion, the dorso-lateral and the ventro-mesial, can be determined; these boundaries are shown in figs. 34 to 37 and in fig. 83.

While these two divisions of the ganglion in the early stages are fused and their boundaries are difficult to determine, there is no difficulty in following the history of the lateral mass up to the time that the definitive ganglia appear. The principal variation which I have observed is in the length of the dorso-lateral portion which is always better defined than the ventro-mesial and sometimes extends well forward over the geniculate; in other cases it is quite short. One of the principal difficulties in determining definite boundaries in the lateralis VIIth ganglion comes from the fact that the root of the geniculate extends throughout the whole length of the lateralis VIIth and enters the brain at almost the same point as the root of that ganglion.

The general appearance and form of the Gasserian and lateralis VIIth ganglia resemble closely the conditions as described by Miss Beckwith ('07) in *Amia*, although she did not describe stages sufficiently early to determine whether the so-called neural crest arises along with the auditory vesicle as the lateral portion of the neural plate or whether the auditory vesicle arises as a thickening of the lateral epidermis and the neural crest as a more dorsally situated derivative of the epidermis. The tendency of the masses out of which the Gasserian and geniculate ganglia later form to break down first into loose tissue seems to be present in *Amia* also.

The origin of the Gasserian ganglion, which is a pure general cutaneous ganglion, and of the lateralis VIIth, which is a pure acustico-lateralis ganglion, from the lateral mass in adjoining

segments receives its best explanation in the interpretation given to the acustico-lateralis system as a special cutaneous system. This system is a special cutaneous system in the sense that its center in the medulla, the tuberculum acusticum, is a specialized derivative of the dorsal horn, or general cutaneous column, of the cord (Johnston '05*b*). While the ear and the lateral line organs are unique in structure and function and the acustico-lateralis fibres can be distinguished from general cutaneous, the two systems stand in the relation indicated above on account of the relation of their central endings. This view is materially strengthened by the fact that the ganglia of both systems in the case of the Vth and lateralis VIIth have similar modes of origin.

Owing to the intimate relation of the auditory vesicle and placodes with the lateralis VIIth ganglia, structurally and in point of time, I shall leave that portion of the lateral mass anterior to the lateralis VIIth and posterior to the Gasserian ganglion, *i.e.*, the communis VIIth or geniculate ganglion to be taken up in connection with the epibranchial ganglion of the VIIth nerve. From the time that the lateralis VIIth assumes definite form until the visceral VIIth appears this remnant can be located but not sharply defined. It lies just over the mesoderm of the hyoid gill bar and is somewhat denser than the more dorsally situated mesectoderm but does not differ sufficiently from either the mesectoderm or the mesoderm to enable one to determine its exact boundries. It is less dense than the more ventrally situated mesoderm.

THE AUDITORY VESICLE AND AUDITORY GANGLION

It is not necessary to descibe the auditory vesicle in detail but I have examined it carefully to determine if there is present any portion of the lateral mass in this region in addition to that portion forming the auditory vesicle and also to determine the exact mode of origin of the auditory and lateralis IXth ganglia. I find that the whole of the lateral mass in the auditory region is converted into the vesicle and that the greater portion of the auditory ganglion comes from the anterior end of the vesicle, but that the ganglion lies in such close proximity to the lateralis VIIth that

it is not possible to determine definitely whether there are lateral mass cells in the VIIIth or not, since it does not become distinct from the lateralis VIIth for some hours. Fig. 6 is characteristic of the median portion of the auditory vesicle before a definite cavity appears, at which stage it resembles the pre- and postauditory placodes (figs. 14, 45). The ventral portion of the vesicle is at this stage (fig. 6) well defined, while the dorsal portion is not yet fully differentiated from the lateral mass. The character of the lateral mass in the anterior third of the vesicle at this stage is quite like that of fig. 5 which is taken just posterior to the auditory vesicle. At the extreme posterior end where the differentiation into dorso-mesial and ventro-lateral or placodal regions has not yet appeared it resembles the condition shown in fig. 3. The ventral and mesial portions of the vesicle (fig. 6) are characterized by having elongated radially arranged cells with their nuclei situated at the periphery. Ventro-laterally the elongated cells pass gradually into the epidermis. Dorsally, however, the elongated radially arranged cells pass into a mass of irregular cuboidal cells which on its ventral border is faintly delimited from the neural tube but dorsally becomes continuous with the tube.

The next figure (12, Stage VII), taken from a slightly older embryo, shows that this mass is practically all incorporated into the vesicle, there being a few scattered cells that possibly may be converted into mesectoderm. As to the fate of the cells connecting the vesicle with the medulla there is another possible way in which they may be disposed of, that is, they may be incorporated into the medulla. There is no way of determining whether this is done, however, and the appearance indicates that they become part of the vesicle. The important fact here is that there are no lateral mass cells left in the region of the vesicle that could be homologous with the neural crest of other authors. Fig. 12 is typical for the whole length of the vesicle at this stage.

In comparing Koltzoff's ('02) and Johnston's ('05b) work on *Petromyzon* attention was called to the fact that the only point of disagreement was in regard to the presence of a neural crest which Koltzoff finds in the auditory region, and that an examina-

tion of the literature throws little light on the question. Dohrn ('90), however, taking this matter up specifically states that the neural crest is present at first in the auditory region but that it disappears. It was hoped that *Ameiurus* would throw light on the question, but the fact that there is no specific neural crest in *Ameiurus* renders my conclusions somewhat unsatisfactory in this matter. Since, however, there is no remnant of the lateral mass left in the auditory region after the vesicle forms, we may conclude that whatever the relation of the neural crest of other types to the lateral mass of *Ameiurus* the position taken by Dohrn is strongly supported by the evidence from this type and I find myself in agreement with Johnston ('06) when he states that the neural crest is absent in the auditory region. This statement will not hold for the region immediately anterior to the auditory vesicle, as was shown in describing the differentiation of the pre-auditory lateral mass. The lateral mass there furnishes the two lateralis ganglia of the VIIth nerve.

The exact mode of origin of the VIIIth ganglion is complicated by the fact that, while it seems to come almost entirely from the anterior end of the auditory vesicle, it develops in such close proximity to the preauditory lateral mass which gives rise to the lateralis VIIth ganglia and is so closely fused with the ventromesial ganglion of these two ganglia that it is impossible to be certain of its exact composition. In the stage in which the auditory vesicle is first recognizable by the radial arrangement of its cells there is no mass of cells occupying the position of the future auditory ganglion; this, when it appears as a definitive mass, is situated as a cap of cells adhering closely to the ventral and ventromesial portion of the anterior portion of the vesicle and extending slightly beyond the anterior end. Here it comes into contact with the irregular mass of cells which differentiates later into the lateralis ganglia of the VIIth nerve. At this stage before the appearance of the auditory ganglion and up to the time the preauditory placode separates from the vesicle the anterior walls of the vesicle are well defined and there is no evidence that cells are being proliferated from it. However, shortly after the separation of the preauditory placode from the vesicle the walls of the anterior

end of the vesicle lose their characteristic regular outline, while throughout the remainder of the vesicle its walls are still characterized by their clean cut boundary and by the presence of a single row of distally located nuclei. At the anterior end, however, the ventral wall becomes indistinguishable and its nuclei become several layers deep and there is no perceptible boundary between the vesicle wall and the forming VIIIth ganglion.

Fig. 13, Stage V, taken from the same embryo as figs. 10 and 11, lies four sections back of the anterior end of the auditory vesicle. The mingling of the vesicle and ganglionic cells and the numerous mitotic figures in this location indicate without doubt that the vesicle contributes cells to the ganglion. If it were not for the fact that the vesicle is constantly in contact with the ganglionic mass derived from the lateral mass, the lateralis VIIth ganglion, and seems to grow forward into this mass on its dorsal and mesial wall, one would be inclined to think that the whole auditory ganglion came from the vesicle. The conditions here are identical with those at the posterior end of the vesicle where the lateralis IXth ganglion is formed. That ganglion is proliferated from the wall of the vesicle after the vesicle is formed and can be followed from its first appearance until the vesicle ceases to contribute cells to it. The conditions at the posterior end of the vesicle are not complicated to the same extent by the presence of any contiguous ganglionic mass and one can be much more certain that the whole ganglion comes from the vesicle. Since, however, at the anterior end of the vesicle the cells derived from the vesicle are in contact with those derived from the lateral mass and there is no definite division into an VIIIth ganglion and two lateralis VIIth ganglia for some time after this, it is impossible to say positively that the whole of the VIIIth is derived from the vesicle. This mode of derivation is indicated by the conditions, however, and is further strengthened by the positions of the lines of cleavage separating the VIIIth from the lateralis VIIth which appear later, as well as by the manner in which the VIIIth ganglion adheres to the vesicle for a long time (figs. 35 to 39 and fig. 83).

I shall defer a discussion of the various ways in which the acustico-lateralis system of ganglia arises until after the description

of the origin of the lateralis Xth. The fact that there may be lateral mass cells in the VIIIth, however, does not affect the homogeneity of this system of ganglia, since the acustico-lateralis system is based on anatomical and physiological characters. We have lateralis ganglia, as in the case of the VIIth, derived solely from the lateral mass, probably from the neural crest in other types, and on the other hand lateralis ganglia, as in the case of the lateralis Xth to be described later, derived solely from the postauditory placode which is the posterior extension of the auditory vesicle. The VIII may be intermediate between these two extremes, since it possibly derives cells from both sources. The diversity in mode of origin shown by acustico-lateralis ganglia emphasizes the fact that the ultimate basis for the establishment of this system of ganglia and nerves rests on anatomical characters and on the central connections of this system in the brain and not on embryological evidence, since some of its ganglia come directly from the lateral mass like the general cutaneous ganglia, while others arise secondarily, coming from the auditory vesicle or placodes, and show a more specialized mode of origin.

There is a great deal of variation in the extent to which these three ganglionic masses (VIIIth and two lateralis VIIth) become separated from each other at any given stage. Sometimes the dorso-lateral VIIth is free at one or both ends, while in other embryos of the same age one or both ends may be incompletely separated from the adjoining ganglia. There is also much variation in the relative lengths of the two divisions of the lateralis VIIth, the dorso-lateralis VIIth sometimes extending far forward on the lateral surface of the Gasserian. Up to the 86-hour stage which I have plotted and in which the three divisions are isolated (fig. 83) the variations strike one as representing different degrees of isolation simply, and in this stage are in such a condition as Herrick ('99) describes for the acustico-facial complex in *Menidia*. After the 86-hour stage the ganglia seem to be in various stages of assembling into the adult condition of *Ameiurus* in which they are much more closely fused than in *Menidia*. In fact, the 86-hour stage of *Ameiurus* seems to be in about the same condition as the adult ganglia of *Menidia*.

THE FATE OF THE PREAUDITORY PLACODE

Under the term preauditory placode I include the anterior extensions of the auditory vesicle from the point where the vesicle narrows at its future anterior boundary to the extreme anterior limit of this extension. At the time when the anterior and posterior boundaries of the vesicle can first be determined by the radial arrangement of its cells and by the size of the vesicle, the placode is represented by a slightly differentiated region in the ventral portion of the lateral mass. Fig. 4, Stage III, is taken four sections anterior to the auditory vesicle; at this stage the preauditory placode occupies the whole of the ventral portion of the lateral mass. Its shortest diameter lies in the dorso-ventral plane and the walls of its cells are quite distinct. The mesial surface of the placode is in contact with mesectoderm cells which seem to have been proliferated from its surface in this early stage. Farther forward (fig. 9, Stage III) the placode is reduced in size and its separation from the lateral mass is less distinct. Slightly anterior to this point it can no longer be detected, having merged completely with the remainder of the lateral mass.

The later history of this placode shows that for a time it becomes more definite in appearance, simulating closely a lateral line organ and on a small scale the changes in the auditory vesicle, and then later disappears entirely, the greater portion of it being converted into mesectoderm. It does not give rise to either ganglia or lateral line organs. The lateralis ganglia anterior to the vesicle can be located before the preauditory placode disappears and the preauditory lateral line organs do not appear for some hours after the disappearance of the last remnant of the placode. The first trace of lateral line organs in *A. melas* appears in an embryo of 75 hours. There is no trace of the preauditory placode left in an embryo of 49 hours. In *A. nebulosus* the last trace of the preauditory placode disappears some hours before this (Stage V), so that there is a period intervening between the disappearance of the last trace of the preauditory placode and the appearance of the first primordium of the preauditory lateral line organs of more than 26 hours..

The process of disappearance is as follows: When the preauditory placode is at its maximum size it extends from the anterior end of the auditory vesicle as far forward as the point where the hyoid gill pocket comes into contact with the ectoderm. Its posterior end is at first continuous with the auditory vesicle and its anterior end gradually thins out into ordinary epidermis. Fig. 14, Stage IV, is taken just anterior to the auditory vesicle at a time when the placode is at its maximum size. The radial arrangement of the cells of the placode and the partial formation of a cavity corresponding to the cavity of the auditory vesicle are evident. This figure should be compared with fig. 6, Stage III. In fact, in some series there is a small cavity in the placode corresponding to that of the auditory vesicle. The first change of a retrogressive nature that I can detect is illustrated in fig. 15, which is taken from the opposite side of the same embryo. Here there is an area corresponding to the thickness of one section intervening between the posterior end of the placode and the anterior end of the auditory vesicle. Here the placode seems to have broken down into mesectoderm, since we have only mesectoderm with a trace of the ventral portion of the placode left, where on the opposite side the placode and vesicle are continuous. The irregular outlines of the posterior end of the placode and of the anterior end of the vesicle also indicate that the placode has been converted into mesectoderm and that the two structures have not simply been carried apart by the growth of the embryo. It is not likely that the placode has moved forward bodily, since the anterior end remains constant in position.

In the next stage sketched from an embryo of the same age but slightly more developed, there is an area of six sections intervening between the posterior end of the placode and the anterior end of the vesicle where the placode has been converted into mesectoderm. The placode here (fig. 16, Stage IV) differs somewhat in appearance, being longer in its dorso-ventral axis and resembling less the auditory vesicle. While the nuclei are still situated in the inner extremities of the cells, the placode has the appearance of columnar epithelium. In a somewhat older series (fig. 17,

Stage V) the placode at this point has broken down almost completely into mesectoderm. The former position of the placode (*Ep*) is indicated by the slight elongation of the remaining cells and the presence of the small cavity which frequently exists on the outer surface between the elongated cells and the flattened layer of the epidermis. This section is taken nineteen sections anterior to the auditory vesicle and there is an area of 18 sections between the anterior end of the vesicle and the posterior end of the placode in which the placode has been converted into mesectoderm. The fate of the anterior remnant of the preauditory placode is somewhat peculiar. It never extends beyond the hyoid gill pocket in any stage. The region just posterior to the gill pocket is where the proliferation of cells takes place to form the epibranchial ganglion of the VIIth nerve. This epibranchial placode, as will be shown later, begins as a thickening of the epidermis differing somewhat in appearance from the disappearing preauditory placode; but it is difficult to determine the exact relation of the last trace of the preauditory placode to the first trace of the epibranchial placode arising in the same area. A valid reason for considering the disappearing preauditory placode as distinct from the early stages of the epibranchial placode of the VIIth nerve lies in the difference in histological character of the two structures. The last stage of the preauditory placode in which it can still be recognized as such has elongated cells with nuclei placed on the inner border and shows no mitotic figures, while the early stages of the epibranchial placode has its cells irregularly arranged and mitotic figures in all stages are very frequent. Fig. 18 from the same embryo as that from which fig. 17 is taken lies six sections anterior to fig. 17 and two sections from the posterior end of the point of contact of the hyoid pocket with the epidermis, the contact of the pocket with the epidermis extending over eleven sections. The resemblance to the placode is still noticeable, the cells being elongated and, except at the central portion being only one cell deep. There are no mitotic figures present at this stage. This figure represents the last recognizable trace of the preauditory placode.

THE ORIGIN OF THE GENICULATE GANGLION

Owing to the fact that both in point of time and in position there is such a close relation between the epibranchial ganglion of the VIIth nerve and the disappearing preauditory placode and that the cells derived from the epibranchial placode combine with cells from the lateral mass to form the definitive communis or geniculate ganglion of the VIIth nerve, it will be more convenient to describe the origin of the geniculate ganglion here than to follow the natural order and take up the differentiation of the post-auditory lateral mass. The series of figures (19 to 24, Stage VI) is taken from an embryo slightly older than the preceding, and in it the last trace of the preauditory placode has disappeared and the thickening which later gives rise to the epibranchial VIIth is just forming. Fig. 19 is taken at the point of contact of the hyoid endodermal pocket, with the epidermis and corresponds in position to fig. 18. It differs in two important respects; the epidermis dorsal and ventral to the contact with the endoderm shows no resemblance to the preauditory placode but is composed of cells whose outlines are very indistinct and whose nuclei are irregularly arranged. In addition to the disappearance of the placode in the region just mentioned, at the point of contact with the endoderm, the epidermis is closely fused with it and presents the appearance of being about to disappear entirely. This gill slit does not open completely in any of my series but the two layers of endoderm do separate in one of them, presenting the exact appearance of an open gill pocket. Fig. 20 is taken four sections posterior to fig. 19 at the point where the contact of the endoderm with the epidermis ceases and it is characterized by the irregular arrangement of its epidermal nuclei, some of which appear to have been proliferated mesially but are still in contact by cytoplasmic strands with the epidermis. Figs. 20, 21, 22, 23 are consecutive sections and lie just behind the point of contact of the gill pocket with the epidermis. In figs. 21 and 22 a proliferated mass of cells, quite small, is isolated slightly from the epidermis. The earliest stage of the epibranchial placode of the VIIth nerve is indicated by the thickened epidermis shown in these figures.

Tracing the placode back in a number of series leaves no doubt that this is the primordium of the placode. The manner in which this thickening of the epidermis increases in size and finally becomes detached, forming a portion of the geniculate ganglion, is quite easy to follow. Of the fate of the small mass of cells (*x*) shown in figs. 21 and 22, I am not certain. They may enter into the ganglion, but it is more probable that they become converted into mesectoderm. They lie a little anterior to the point of origin of the ganglion, and there is in some of my later series a small mass of cells anterior to the point of contact of the gill pocket with the epidermis, which resembles these, but their origin and fate I cannot determine definitely. If the cells shown enter into the ganglion, it is by attaching themselves later to the main ganglionic mass derived from the placode. Of this, however, I have no evidence.

Figs. 22 and 23 show a typical appearance of the early stage of any epibranchial placode and resemble closely the first stages of the placodes of the IXth and Xth epibranchial ganglia. The nuclei are several layers deep and quite irregular in arrangement and mitotic figures are beginning to be quite numerous. Fig. 24 is taken four sections posterior to fig. 23 and shows the transition of the placode into ordinary epidermis. Here, however, mitotic figures are still rather numerous but two sections posterior to this the epidermis is unmodified.

A comparison of the embryo from which figs. 19 to 24 (*A. nebulosus*, Stage VI) were taken with the one from which figs. 17 and 18 (Stage V) were taken leaves little doubt that, while the epibranchial placode appears practically in the place where the preauditory placode disappeared, there is no direct relation between the two histologically. All of the preauditory placode posterior to the hyoid gill pocket is converted into mesectoderm and, while there is no evidence that the placode at the point of contact is ever converted into mesectoderm beyond the presence of the small mass of cells mentioned above, the fact that a contact with endoderm is formed would obscure the conditions here somewhat. While it is impossible to say that none of the cells that were once a part of the preauditory placode or their direct descendants enter

into the primordium of the epibranchial placode, the histological differences of the two structures and the fact that the one differentiates after the other has lost its characteristic structure show that the relation of the two placodes is more apparent than real. Added to this we have the evidence to be shown later that there is absolutely no relation between the postauditory placode and the epibranchial placodes of the IXth and Xth nerves.

The condition of the epibranchial placode in a somewhat older embryo in which the placode is still in contact with the epidermis is shown in figs. 25 to 30 (*A. nebulosus*, Stage VII). Fig. 25 is taken just posterior to the point of most intimate contact of the hyoid gill pocket with the epidermis. In this series the contact of the hyoid pocket with the epidermis, similar to that shown in fig. 19, (Stage VI) occupies only one section, while in the series from which fig. 19 was taken the contact is four sections in length. The hyoid pocket after coming into intimate relation with the epidermis gradually withdraws, and in the next stage following that from which fig. 25 was taken no longer reaches the epidermis at all.

Fig. 25 is taken at the extreme anterior end of the placode and the placode here differs from the epidermis anterior to it only in being somewhat thicker and in having its nuclei irregularly arranged in more than one row.

Fig. 26 is taken from the next section posterior to that from which fig. 25 was taken and there is here a decided thickening of the epidermis with numerous mitotic figures in various stages. In the next section (fig. 27) the thickening projects mesially as a well defined mass of cells and there are no less than twelve cells in various stages of mitosis in the placodal region of the epidermis. In the succeeding section (fig. 28) the proliferated mass of cells, the anterior portion of the future epibranchial ganglion, is larger and contains mitotic figures in addition to those in the epidermis. The ganglion is still attached to the epidermis in all these areas by a pedicle fully as thick as the ganglion itself. Two sections posterior to this point (fig. 29) the ganglionic proliferation changes somewhat in appearance, being longer and its attachment involving more of the epidermis ventral to it, so that

it passes gradually into the epidermis here, while on its dorsal surface it passes suddenly into rather thin epidermis. The appearance in this section indicates that the cells contributed to the ganglion before its detachment come mainly from the epidermis situated ventrally to its point of attachment. This conclusion is verified from a study of the epibranchial placodes of the IXth and Xth ganglia. The whole of the ganglion shown in fig. 29 is not derived from the placode. The portion situated mesially and dorsally (*L. M. G. VII*, fig. 29) is derived from the remains of the lateral mass lying anterior to the lateralis VIIth ganglion. The separation between these two constituents of the ganglion is faintly indicated in the figure. The presence of these lateral mass cells can be first detected in the section preceding the one from which fig. 29 is drawn and the separation is there somewhat more distinct than in the section sketched. In the section following the one from which fig. 29 was taken (fig. 30) the division between the two constituents is quite apparent and the portion of the ganglion derived from the lateral mass is slightly larger than the placodal constituent. A few sections posterior to this point the placodal portion of the ganglion ceases to be present, while the lateral mass portion reaches its maximum size in this embryo.

The posterior end of the lateral mass portion of the ganglion cannot be definitely determined, since at this stage it simply becomes looser in texture and finally before reaching the region of the lateralis VIIth can no longer be distinguished from that ganglion and from the ventrally situated mesoderm. The fact that this ganglionic mass is at its posterior end rather closely applied to the ventrally situated mesoderm makes it impossible to determine the exact boundary posteriorly before the ganglion assumes definite shape, as it does a little later after the detachment of the placodal portion; in addition to this fact the fibrillated root of the whole ganglionic mass appears at the posterior end of the ganglion and the point where this appears is in most of the cranial ganglia preceded by a more or less ill-defined mass of cells which renders the determination of exact boundaries difficult.

At this time the future ganglion consists of two constituents, first a placodal constituent proliferated from the thickened epidermis or epibranchial placode which is largest in its middle region and becomes smaller both posteriorly and anteriorly and is everywhere still attached to the epidermis although it later becomes completely detached. Secondly there is a lateral mass constituent lying on the dorso-mesial portion of the placodal constituent and ending posteriorly in loose lateral mass cells so that at this stage its posterior boundary cannot be definitely determined.

As the geniculate ganglion becomes larger the difference in size between the body of the ganglion and its root enables one to determine approximately the posterior extremity of the ganglion. This can be done with certainty only when the fibrillated root appears. At this time the trigemino-facial complex has the arrangement indicated in fig. 83 when the Gasserian and geniculate ganglia overlap for about one-half the length of the Gasserian. This overlapping is due apparently mainly to the forward growth of the geniculate on the mesial side of the Gasserian, the root of the Gasserian remaining constant in position and the body of the ganglion extending only slightly posterior to its original position. The forward extension of the geniculate is probably entirely due to growth in size of the ganglion, since I can find no evidence of the further proliferation of cells anterior to the point occupied by the placode.

Both the Gasserian and geniculate ganglia assume a definite form with well defined boundaries rather slowly, so that for some time they consist of condensed masses of cells with irregular outline. Since the extent of fusion of the acustico-facial complex is very great in the adult in *Ameiurus*, I have given a series of figures (31 to 39) to show the condition of the ganglia at a time when all the components are still separate and the roots and chief trunks of the nerves derived from these ganglia are still distinct. These figures are taken from the same embryo (*A. melas* 86 hours) as that from which fig. 83 was constructed. This plot should be compared with fig. 2 of Herrick's paper ('01). The principal point of interest here lies in the fact that the roots and chief

trunks derived from these ganglia are found to contain only general cutaneous or communis or lateralis fibres.

Fig. 31 is taken through the origin of the trunk of the Gasserian ganglion, and fig. 32 just anterior to the point where the trunk of the geniculate ganglion leaves the ganglion, and consequently lies between the trunks of the Gasserian and geniculate ganglia. These two trunks are entirely separate not only at their point of origin but throughout their whole course at this time. They form the supero-lateral and infero-mesial strands respectively of Wright ('84*b*). These combine and later separate to give rise to the maxillary and mandibular trunks which are mixed, containing general cutaneous, visceral, and lateralis components. Herrick ('01, p. 183) could not determine positively that these two strands were pure but there can be no doubt that they are pure at this stage and that the supero-lateral strand contains fibres from the Gasserian ganglion only and that the infero-mesial strand contains fibres from the geniculate ganglion only. Further, the roots are not yet in contact at any point nor do they contain lateralis fibres as yet.

Figs. 33 and 34 are taken through the root of the Gasserian ganglion and show that the root is no less distinct than the trunk. The dorso-lateral lateralis VIIth also appears in these sections. The roots of the geniculate and Gasserian ganglia are separated by 15 sections, while the trunks at this stage are six sections apart. The overlapping of the ganglia finally brings the trunks into the same plane but even then there can be no doubt that they are derived separately from their respective ganglia.

Fig. 35 is taken through the origin of the hyomandibular nerve (*T. V. L. VII*) which is at this time a pure lateralis nerve derived from the ventral lateralis VIIth ganglion (*V. L. VII*). This nerve later contains in the adult small strands of general cutaneous and visceral fibres (Herrick, '01) but is at first a pure lateralis nerve. The ramus oph. sup. VII is in the adult a pure lateralis nerve. In this stage it can be detected as a forward extension of the anterior end of the dorsal lateralis VIIth ganglion but it is only faintly fibrillated. The ramus oph. sup. V, I cannot detect at this stage but it is probably mixed at an early stage, since the

Gasserian and geniculate ganglia from which it derives its two components lie side by side and their anterior ends from which the nerve arises are intimately in contact when it can first be detected. The arrangement of the roots of the geniculate, lateralis VIIth and auditory ganglia are shown in figs. 36 to 39. They are all quite distinct and can be followed to the point of contact with the medulla.

As mentioned above, from this time on the components of the Vth and VIIth ganglionic complex become more intimately fused so that it is not surprising that nerve trunks which are at first undoubtedly pure trunks, *i.e.*, contain only one component, later become mixed and contain two or more components. The contiguity of the ganglionic masses furnishes a basis for the mixing. Those components which are not found in the nerve at first must grow into it later. They are unquestionably there in the adult and not there in the embryo. The geniculate ganglion wedged in between the Gasserian and lateralis VIIth ganglia is in a particularly favorable position to send its fibres into nerves derived primarily from other ganglia. This has gone so far in *Ameiurus* that 12 out of 14 of the chief nerves coming from the acustico-facialis complex contain visceral fibers, as compared with five in *Gadus* and *Menidia*.

There are, at least, three methods by which nerves become mixed. The first is illustrated by the maxillary and mandibular trunks which arise some distance from the ganglion, after the fusion of two pure strands, the supero-lateral which is pure general cutaneous and the infero-mesial which is pure visceral. These pure strands after coming into contact break up into two mixed nerves, the maxillary and the mandibular. A second method by which nerve trunks become mixed is illustrated by the hyomandibular which is at first a pure lateralis nerve but later becomes mixed by having general cutaneous and visceral fibres grow into it from their respective ganglia. A third method is illustrated by the rami oph. sup. V and VII which, owing to the contiguity of its ganglia, the Gasserian and geniculate, seems to be mixed from the first, the roots growing out from the ganglia in contact with each other.

DIFFERENTIATION OF THE POSTAUDITORY LATERALIS MASS

The changes which take place in the lateral mass posterior to the ear resemble in a general way those which take place anterior to the ear. The postauditory lateral mass gives rise to a post auditory placode situated ventro-laterally, continuous with the auditory vesicle, while the dorso-mesial region breaks down into a loose mass of cells which is converted partly into mesectoderm and partly into the general cutaneous and general visceral ganglia of the Xth nerve. As mentioned above, the lateral mass is at first entirely homogeneous. Fig. 3 represents the appearance throughout its whole extent at an early stage, except that the lateral thickening is slightly less marked as it passes into the region of the spinal cord.

The first evidence of differentiation posterior to the ear is shown in fig. 5 (A. nebulosus, Stage III) which is taken four sections posterior to the posterior end of the auditory vesicle. There is noticeable here a slight distinction between the ventro-laterally situated postauditory placode and the dorso-mesial region. The separation between these regions is indicated by the mode of contact of the cell walls on either side of the dividing line and by the appearance of a vacuole. This sketch is taken from the same embryo as that from which figs. 4, 6, 7, 8 and 9 were taken. The differentiation of the preauditory lateral mass is only slightly in advance of that of the postauditory mass. The changes in the dorso-mesial portion of the postauditory mass by which it becomes converted into mesectoderm resemble closely those that take place in the region of the Gasserian ganglion. On either side of the Xth ganglion the dorso-mesial portion of the lateral mass becomes converted into a very loose mass of mesectoderm, except at its ventral border; here where it comes into contact with the mesoderm it remains slightly denser.

In the region where the Xth ganglion forms and possibly where the IXth forms the process of conversion into mesectoderm does not go so far and the lateral mass in these regions is in some embryos slightly denser than in the surrounding regions. These two regions however are only slightly denser and, in a stage fol-

lowing the breaking down of the dorso-mesial portion of the lateral mass present the appearance of not having broken down so completely as surrounding areas. A comparison of figs. 40 to 43, (*A. nebulosus*, Stage VII) all from the same embryo, brings out these relations in an embryo in which the ganglionic regions are unusually well marked. Fig. 40 is taken one section posterior the auditory vesicle. The whole region between the cord and the endoderm is occupied by the derivatives of the lateral mass. Just dorsal to the endoderm (fig. 40, *Y*) the tissue is somewhat dense and there is also a slight condensation (fig. 40, *G*) at the level of the upper third of the medulla; this condensation extends into the next section (fig. 41, *G*) but disappears in the section following that from which fig. 41 was taken. From this point back to the region where the Xth ganglion appears the lateral mass presents the appearance shown in fig. 42. The mesectoderm presents the appearance of mesenchyme having well defined nuclei but with ill-defined cytoplasmic branches forming a loose network. Just over the mesoderm the derivatives of the lateral mass in all three figures are somewhat denser. It will be recalled (pp. 330-331, 345) that it is this portion of the lateral mass that forms the Gasserian and geniculate ganglia in the preauditory region.

Figure 43 is taken through the region of the Xth ganglion just anterior to the anterior end of the lateralis Xth. This section is taken just back of the anterior end of the ganglionic mass (*J. G. X*, fig. 43). The anterior end of the ganglion lies somewhat nearer the medulla than in the section figured, while posterior to this point the mass is found more ventral and lateral in position, finally coming into contact with the denser portion indicated in figs. 41 and 42, (*Y*), lying just over the mesoderm. The loose mass of cells shown in fig. 43 (*J. G. X*) gives rise to the jugular ganglion to be described later.

Like the early stages of the Gasserian ganglion, the whole mass is extremely ill-defined with irregular borders passing gradually into the surrounding mesectoderm. The ganglionic mass does not reach the dorsal portion of the medulla and there is no indication of a migration of cells from that structure.

At this stage in the formation of the ganglion there is nothing to indicate its presence except the slightly denser massing of the cells and the somewhat denser character of the inter-nuclear material. There is one rather striking difference between the Xth and preauditory ganglia. Anterior to the ear all the ganglia trend down and forward from their points of attachment to the brain where the fibrillated roots will appear. The Xth ganglion derived from the lateral mass in the same manner trends down and back from the point where its fibrillated root will appear, reversing the relations to the medulla. These figures are taken from an embryo in which the condensations in the region of the IXth and Xth ganglia are usually well marked. From this stage up to the seventy-fifth hour in *A. melas* there is no well defined ganglion even in the region of the Xth, and in several series I can find no evidence of either ganglion. Between the 49-hour and the 56-hour embryo, *A. melas*, there is nothing that can be identified positively as a Xth ganglion, although one can be quite sure of the region in which it ought to be located. In embryos of 61 to 65 hours, *A. melas*, there are slight condensations in the region of the Xth, but they would hardly be detected if one did not read back from older series. The ventral derivative of the lateral mass (Y, figs. 41, 42) is present in the region of the Xth during this time, however, and it is this region which furnishes the greater portion of the visceral Xth. During the whole time under discussion the lateralis Xth ganglion is present and furnishes a good landmark in the attempt to locate the early stages of the visceral Xth.

By the seventy-fifth hour (*A. melas*), the ventral portion of the Xth ganglion derived from the lateral mass has assumed a definite form and can be followed from this time on easily. It occupies at this stage a ventro-mesial and mesial position with reference to the lateralis Xth which is an elongated cylindrical mass of cells with quite definite boundaries. The visceral Xth extends from near the anterior boundary of the lateralis Xth to a point beyond its middle portion and the motor root of the Xth extends along the mesial side of the lateralis Xth running forward and upward to the medulla. At this stage the lateral mass ganglion of the Xth is

situated low in the body on a level with the dorsal portion of the gill slit and is connected with the medulla by the narrow strand of loose cells described above. The outline of the ganglion is still indefinite and its ventral portion is closely applied to the mesoderm underlying it. All of the visceral portion of the Xth except that derived from the placodes seems to come from the ventral portion of the lateral mass, while the jugular or general cutaneous ganglion comes from the dorsal portion. The jugular ganglion cannot be detected for some time after the visceral Xth is formed.

Owing to the intimate relation of the lateral mass portion of the Xth ganglion to the epibranchial placodes, it will be better to describe the lateralis Xth first and return to the visceral Xth later (p. 79). The fate of the lateral mass cells in the region of the IX ganglion will be taken up with the lateralis IXth. The relation of the visceral Xth ganglion to the jugular or general cutaneous Xth which appears later and is situated near the medulla intra-cranially, is extremely interesting. It will be recalled that the lateral mass anterior to the ear gives rise to the Gasserian, a pure cutaneous ganglion, and to a part of the geniculate, a visceral ganglion which fuses with the ganglion from the epibranchial placode. Both these ganglia become closely fused in the adult and are situated intra-cranially. In the Xth, however, we have a complete separation of the general cutaneous and visceral portions; the former being small and situated intra-cranially, the latter large and situated extra-cranially and fusing with the placodal ganglion just as the geniculate does. From evidence to be brought out later it appears that the lateral mass contingent of the geniculate and visceral Xth is really a general visceral component, the special visceral or gustatory ganglia being derived from the placodes. In types having a well defined neural crest these same relations would seem to hold, *i.e.*, the general cutaneous and general visceral ganglia of the head have a common derivation from the neural crest, which is homologous with the neural crest of the spinal cord. The chief difference between the brain and the cord in this respect lies in the greater size of the cranial ganglia and the extent to which the general cutaneous component and general visceral component, which are both represented in the spinal ganglia,

are separated in the head. In the more generalized Xth the general cutaneous is intra-cranial and the general visceral extra-cranial, while in the more highly specialized region of the Vth and VIIth both are intra-cranial.

THE ORIGIN OF THE LATERALIS XTH AND THE EARLY STAGES OF THE POSTAUDITORY PLACODE

The lateralis Xth is derived not from the lateral mass but from the postauditory placode as it moves away from the auditory vesicle. The first evidence I find of a separation between the postauditory placode and the auditory vesicle is shown in fig. 44, Stage IV. The dorsal portion of the auditory pit was present in the preceding section. In fig. 44 only the ventral portion remains as the placode. The portion which disappears is that most nearly in contact with the medulla. In the following section (fig. 45) the placode has lost all connection with the dorso-mesial portion of the lateral mass which is beginning to be converted into mesectoderm. The length of the placode at this time is only four sections. Fig. 46, Stage IV, shows the appearance of the placode in a series of the same age, but less developed, in which the auditory vesicle is continued into the placode with no break in continuity. The placode is here seven sections long.

The placode now moves back apparently after it is detached from the auditory vesicle. My series is incomplete at this period and I am consequently unable to describe the earliest appearance of the anterior end of the lateralis Xth or the rate at which the placode moves away from the auditory vesicle at first. At the time, however, when the anterior end of the placode has reached a distance of twenty-one sections from the vesicle, Stage VII, the placode has not changed in appearance but the lateralis Xth ganglion is present and has a length of ten sections and overlaps the placode for five sections. Anterior to the region of overlap the lateralis ganglion lies just under the epidermis between it and the mesectoderm as a rather irregular mass of cells (fig. 47). Throughout the whole region of the overlap the placode is contributing

cells to the ganglion. As one reads from the anterior towards the posterior end of the placode, the placode gradually becomes larger until we reach the middle region (fig. 50); it then gradually diminishes in size until it assumes the appearance of the ordinary epidermis. Coincident with the increase in size of the placode in its anterior portion there is a decrease in the number of cells in the overlapping ganglion (figs. 48, 49, 50) until just posterior to the middle (fig. 51) there are no ganglion cells present. This condition is duplicated in all my series in which the ganglion and placode overlap.

In an embryo of $56\frac{1}{2}$ hours (*A. melas*) the placode has moved beyond the posterior end of the ganglion and there is a space of three sections between the placode and the ganglion.

From this time on the placode moves steadily back from the region of the ganglion and as it moves away gradually loses its resemblance to the earlier condition. Its cells cease to have a radial arrangement and it is recognizable simply as a thickening of the epidermis. The appearance of the ganglion anterior to the region of the overlap is shown in fig. 52 (Stage IX). The question as to whether the postauditory placode moves bodily away from the auditory vesicle or whether the placode at successive distances from the vesicle represents a localized differentiation at those points has been variously answered. The anterior end of the placode seems to be partly converted into ganglion cells and partly to revert to ordinary epidermis as far as its appearance is concerned. The posterior end of the placode seems to arise by the conversion of epidermal cells into placodal cells. There is no recognizable train of cells left in the epidermis in the route of the moving placode. The lateral line organs which appear long after the placode has passed a given point appear approximately along the route traveled by the placode, but are not derived from the placode.

The reason for thinking that the placode moves by successive differentiations and does not migrate bodily rests on the fact that in the region of the placode, part of the placode becomes detached as the lateralis Xth ganglion and the remainder not so used is detached or passes gradually into ordinary epidermis, since there is no abrupt transition from placode to epidermis. After

the placode ceases to contribute cells to the ganglion the ganglion ends bluntly posteriorly and there is no strand of cells connecting the ganglion and placode. The trunk of the lateral line nerve of the Xth grows out as a new structure from the ganglion.

THE FATE OF THE POSTAUDITORY PLACODE AND THE APPEAR-
ANCE OF THE LATERAL LINE ORGANS OF THE BODY

After the postauditory placode is no longer in contact with the lateralis Xth ganglion it moves back some distance from the ganglion and remains approximately stationary from the fifty-sixth hour up to the one hundred and thirteenth hour (A. melas), during which time it gradually becomes smaller and less distinct. During the greater portion of this time it can be identified positively both by its appearance and by its position in the body and by the fact that there is nothing else with which to confuse it. In the mean time there have appeared in the region traversed by this placode in its backward movement and in the region from which the auditory vesicle was detached from the ectoderm four lateral line organs. These are the first four described by Herrick ('01, plate xiv, fig. 1). The first according to his nomenclature, which is innervated by the ramus oticus from the VIIth nerve, arises lateral to the anterior end of the auditory vesicle and appears first in my series in an embryo of 105 hours. The auditory vesicle at this time is beginning to form the semicircular canals. The second organ, innervated by the ramus supratemporalis IXth, develops between the posterior end of the auditory vesicle and the anterior end of the lateralis Xth ganglion. It appears first in the embryo of 105 hours. The third and fourth organs innervated by twigs from the lateralis Xth ganglion develop in close proximity to the posterior end of that ganglion from a common primordium which elongates and gives rise to two organs. The anterior portion of the common primordium gives rise to the third organ and the posterior to the fourth organ. This common primordium of the third and fourth organs appears first in an embryo of 86 hours and about nineteen hours before the appearance of the primordia of the first and second organs.

At the time of the appearance of the common primordium of the third and fourth organs the postauditory placode lies about five sections posterior to it and can be distinguished easily from the primordium by the fact that the placode still retains its characteristic appearance, having elongated radially arranged cells, while the primordium bears no resemblance to a lateral line organ, being merely a thickening of the epidermis. Here, as in all other lateral line organs, one must first locate the organ after it is fully formed and then read back in series and locate the primordium. This can be done first by counting sections and second by using convenient land-marks in the body. This is necessary because none of the lateral line organs at first have any resemblance to the adult organs.

In an embryo of 99 hours (*A. melas*) while the postauditory placode is still recognizable as a thickening of the epidermis there have appeared at least two lateral line organs posterior to it. These two organs can be traced continuously in my older sections and lie posterior to the large branch of the Xth nerve, while the placode lies anterior to it. Owing to the fact that structures frequently do not develop uniformly even when a series of graded ages is used, it is not possible to make definite statements in regard to the last stage of the postauditory placode. Of its moving back from the vesicle and of its gradual reduction I am quite sure. In an embryo of ninety-nine hours (*A. melas*) while the third and fourth lateral line organs are still contained in the common primordium the placode is recognizable and back of this are two primordia of lateral line organs. In an embryo of one hundred and five hours the placode is present but no organs lie posterior to it. In an embryo of one hundred and thirteen hours the two lateral line organs previously mentioned as lying posterior to the placode are present in practically the same position as in the embryo of ninety-nine hours, having moved slightly away from the vesicle while the sections occupied by the placode in the preceding series are vacant and remain vacant in later series. These two organs persist in my later series and I infer that the postauditory placode disappears posterior to the position of the

fourth lateral line organ and gives rise to no organs. If any do arise from it it would be the fifth of the body lateral line.

As to the mode of origin of the organs, there seems to be little variation. Each one appears as a slight thickening of the epidermis scarcely perceptible at first except by its location at the seat of the future organ. This thickening becomes more pronounced by the elongation of the deeper cells and by their assuming a radial arrangement with frequently a small circular cavity just beneath the outer flattened layer of epidermis and at the apex of the radially arranged cells. This process of the elongation of the radially arranged cells continues until the organ assumes its permanent form. The variation mentioned above consists in the different rates at which this process is carried on and also the different stages of development at which the organs sink into canals. The facts brought out above differ materially from the usual description of the relation of the dorso-lateral placode to the lateral line organs and lateral line nerve but are in close agreement with the work of Miss Platt on *Necturus* ('95). The fact that anterior to the ear the preauditory dorso-lateral placode disappears more than 26 hours before lateral line organs can be detected and that posterior to the ear at least four lateral line organs appear anterior to the placode, while it can still be recognized as such, leaves no doubt in the writer's mind that there is no evidence of a genetic relation between the dorso-lateral placodes and lateral line organs in *Ameiurus*. The lateral line organs are definite differentiations of the epidermis, just as are the taste buds, and the nerves which supply them grow from specific ganglia just as in the case of the gustatory nerves. There seems to be no doubt that the auditory vesicle and pre- and postauditory placodes are homologous, or rather the same structure, but the relationship of the lateral line organs and vesicle is on a somewhat different footing.

If the auditory vesicle phylogenetically is to be looked upon as containing sensory areas homologous to lateral line organs, in the ontogeny we have the troublesome fact that lateral line organs arise in the epidermis in the same area as that from which the vesicle arose; further than this the preauditory lateral line organs

are innervated from ganglia derived from the lateral mass or neural crest of other types while those posterior to the ear are innervated partly by ganglia derived from the auditory vesicle and partly by ganglia derived from the posterior extension of the vesicle or the postauditory placode.

The foregoing description of the relations existing between the pre- and postauditory placodes and the lateral line organs, differs so much from that of Wilson ('91, '97) in the sea bass and salmon that it merits a fuller discussion. The accounts differ as to the mode of origin of the lateral line organs, Wilson tracing them to the sensory lines derived from the postauditory placode and the preauditory placode (branchial sense organ of Wilson and Beard) while the present account traces them to differentiations of the epidermis not derived from the placodes. Wilson's statement of the case as given in his short paper on the salmon ('97) is as follows and will stand for the conception of those authors who agree with him. He states that in *Serranus*

The organs of the lateral line, the auditory sac, and the superficial sense organs of the head (presumably all) were derived from a common foundation. This common foundation has the shape of a long furrow (ectodermic) on the side of the head region. The furrow splits into three parts, the posterior part giving rise by division to the organs of the lateral line, the middle part becoming the auditory sac, the anterior part becoming a histologically developed branchial sense organ, situated in front of the single gill slit of the embryo, from which a (sensory) cord of cells is prolonged forwards.

Wilson finds practically the same condition in the salmon except that the pre- and postauditory furrows are only thickenings in this form, and cites Mitrophanow ('93) and Locy ('95) as agreeing substantially with him.

The paper on the salmon is brief and does not describe the exact mode of appearance of the definitive lateral line organs. An examination of Wilson's paper on the sea bass ('91) shows that the relation of the preauditory lateral line organs to the preauditory placode is much less definite than in the paper on the salmon. He

says (p. 246) in discussing the fate of the preauditory placode (branchial sense organ) that "the further development of the organ consists in the loss of its cavity, in histological differentiation, and in the transformation of its ill-defined anterior extremity into two cellular cords which doubtless serve as source for the production of new organs." On the following page in discussing the anterior sensory tract he states that "during larval life one or two sense organs are found in this region and it is extremely probable that they arise from the dorso-lateral tract." In the following paragraph is the statement that "the anterior sensory tract is at the time of hatching very short and just what becomes of it I do not know." This anterior sensory tract is the tract which Wilson derives from the anterior end of the branchial sense organ and which gives rise by its forward extension to two tracts.

It may be well to call attention to the fact that where Wilson makes unequivocal statements in regard to the relation of the auditory vesicle to the preauditory placode, and to the postauditory placode in part, we are in essential agreement, *i.e.*, in the origin of the auditory vesicle and the pre- and postauditory placodes from a common primordium, the detachment of these placodes from the vesicle and in the disappearance of the preauditory placode. Wilson finds that the preauditory placode disappears, while the postauditory continues to grow back giving rise to the lateral line, but I find that both the pre- and postauditory placodes finally disappear. With this exception up to this point the two accounts are quite similar. The presence of sensory cells in Wilson's branchial sense organ and their absence in *Ameiurus* is not a radical difference, especially since the preauditory placode in *Ameiurus* has such a close resemblance to the auditory vesicle.

As to the point of difference, a careful reading of Wilson's paper fails to show a definite relation between the branchial sense organ and the anterior sensory ridges, and the specific lateral line organs. The disappearance of the branchial sense organ and the anterior sensory tract, and the appearance of specific

lateral line organs in the same region is not positive evidence of genetic relationship between the two structures. The divergence in our accounts begins in the description of the method by which the specific lateral organs arise, more particularly as to whether the sensory ridge on which Wilson finds the lateral line organs differentiating is an extension from the pre- and postauditory placodes. In *Ameiurus* I find no common sensory ridge from which the organs differentiate, and can trace the gradual disappearance of the pre- and postauditory placodes. Miss Clapp ('99, pp. 239-251) states that these sensory ridges originate in the auditory region, but nowhere I think traces them to the auditory vesicle or its derivatives, while Miss Beckwith ('07) states definitely in tracing the genesis of the lines that they do not come from the auditory vesicle but arise as local differentiations of the epidermis on which the lateral line organs later appear (p. 28).

There is a bare possibility that the relation of the anterior sensory ridge to the branchial sense organ as described by Wilson in *Serranus* is one of contiguity only and not of genetic relationship. If this be admitted, and it is the point about which Wilson is least definite, then there are no insuperable difficulties in harmonizing the two views, for the lines seen by Allis ('89) and other workers may be interpreted in two different ways. "They might be continuous ridges which break up into individual sense organs, or on the other hand they might be formed by a series of individual sense organ primordia whose extremities become confluent. There is evidence for both views. Wilson is very positive concerning the mode of formation of the postauditory lateral line organs from a common primordium derived from the postauditory extension of the vesicle in the sea bass, while I have evidence which I do not think can be doubted that even the postauditory lateral line organs arise separately and have nothing at all to do with the postauditory placode. This conclusion was reached by Hoffmann ('94) and by Miss Platt ('95, '96) in part of the organs in *Necturus*. The same conclusion is reached by Miss Beckwith in *Amia*. Allis's work ('89) does not really confirm Wilson, since his earliest stage was about one day old (after hatching) and this is too late to

trace the genesis of the sensory lines. Miss Beckwith shows that the lines from which the lateral line organs appear are entirely distinct from the auditory vesicle and that the supra-orbital, sub-orbital and mandibular sensory ridges arise separately. Locy states that he agrees with Wilson but gives no description of the origin of the specific lateral line organs. It will serve to clear the ground for future work if it is remembered that there are two distinct problems here; first, do the pre- and postauditory lateral line primordia grow out from the auditory vesicle or its extensions the pre- and postauditory placodes, and, second, do the lateral line organs appear individually or do they differentiate from a common primordium?

Admitting that the lateral line organs do differentiate in some types from common sensory ridges and in other types as individual organs, the question arises as to which is the more primitive method. If the appearance of individual organs as in *Ameiurus*, each of which is homologous with sensory areas of the auditory vesicle, is the primitive method, it is conceivable that the elongation and precocious appearance of the primordia from which these organs appear (and these primordia are always longer than the organs in *Ameiurus*) might result in a more or less definite line such as Wilson describes in *Serranus* and Miss Clapp in *Batrachus*. The growth of the postauditory sensory line would mean nothing more than the appearance of successive organs whose primordia have become continuous. If the differentiation of organs on lines which are extensions of the auditory vesicle is the primitive mode, it is more difficult to understand how the method by which they arise in *Ameiurus* could be derived from it. It is hard to see how organs that primitively come from a common primordium could later in phylogeny arise singly. The difficulty is increased when we remember that the lateralis VIIth ganglion does not come from the vesicle or any of its derivatives but from the lateral mass (neural crest). Perhaps the greatest obstacle to this view on theoretical grounds arises from the confusion which is introduced into current ideas of the primitive relation of the lateral line organs to the sensory areas of the audi-

tory vesicle. If these organs arise as differentiations of sensory ridges which grow out from the anterior and posterior extension of the auditory vesicle, they cannot be strictly homologous with the sensory areas of the auditory vesicle, since they are derived from it, unless we consider the ear as precociously developed on this ridge. If on the other hand the lateral line organs arose primitively as single organs, the sensory areas of the auditory vesicle and lateral line organs can be considered as homologous and the conditions in *Serranus*, *Salmo*, *Batrachus*, and *Amia* can be explained as modifications of this primitive method.

THE PLACODAL GANGLION OF THE IXth NERVE

The visceral ganglion of the IXth nerve stands in a rather unique position since it has no recognizable constituent derived from the lateral mass, and is therefore a pure placodal ganglion; otherwise it presents many points in common with the placodal ganglion of the VIIth and those of the Xth to be described later. It begins as a thickening of the epidermis on a level with the dorsal limit of the first true gill slit, and extends posteriorly from this point. The thickening is characterized by the irregular arrangement of its nuclei, and by the number of mitotic figures. The stage of thickening is followed by a process of proliferating cells mesially and posteriorly, and this group of proliferated cells is finally detached *en masse* and acquires a connection with the more dorsally situated lateralis ganglion. Fig. 53 from a 56½-hour embryo (*A. melas*) is taken just posterior to the point of contact of the visceral pocket with the epidermis. The placode is recognizable at this stage as a simple thickening of the epidermis extending from the level of the dorsal border of the future gill slit down to the level of the branchial artery and longitudinally occupying three or four sections. The epidermis is several cells thick and usually, especially during later stages, shows many mitotic figures. The epidermis is nearly always slightly indented at the point where the placode appears, but whether this is to be associated with the placode or with the gill slit is not clear. The placode differs structurally from the epidermis adjoining it in the

characters mentioned, and in addition it takes a slightly darker stain and its inner border is usually less ragged than that of the surrounding epidermis. The epidermis anterior and dorsal to the placode rarely has a well defined border on its inner surface, but presents the appearance of proliferating cells into the mesectoderm. The placode passes almost imperceptibly at first on its anterior and posterior borders into the epidermis. On the dorsal surface, however, the transition from placode to epidermis is quite sudden. In the region of the placode, however a well defined mesial border can be seen and, while it could not be said that no cells slip individually from this placode into the mesectoderm, there is no evidence of it.

This process of thickening of the ectoderm is followed a few hours later by a movement of the cells *en masse* into the region of the mesectoderm in a posterior and dorsal direction. Fig. 54, taken at the middle of the placode, shows its appearance in an embryo of 69 hours. It occupies about the same relative position as in fig. 53, but the auditory vesicle which was absent in fig. 53 appears in this section (not shown in the figure, however), owing apparently to its extension backward. The placode has a much denser appearance here than the surrounding mesectoderm and its boundaries can usually be located with no difficulty except at the posterior end which is ill defined, except in the earliest stages before the placode begins to project mesially. The placode is shorter dorso-ventrally than in the preceding stage, and on the side from which the sketch was made not more than four sections long, but on the opposite side as much as seven sections long. On its ventral, anterior, and posterior borders it passes over into ordinary epithelium, as in the preceding stage described. Its mesial projection at the thickest part from which fig. 54 is taken is about three times the thickness of the adjoining epidermis. Cell multiplication is taking place as evidenced by the presence of mitotic figures; in fact, there is evidence of both cell migration from the epidermis after the placode begins to project mesially, and of the development of cells *in situ* in the projecting portion of the placode.

In the next series, 75 hours, which I have not figured, little change has taken place, although the placode extends somewhat farther mesially; but in an embryo of 81 hours (fig. 55) a change can be noticed. Figs. 55, 56, 57 are consecutive figures taken from the same embryo. Fig. 55 is taken from the anterior portion of the placode and shows a decided constriction between the ganglionic mass and the epidermis with which it is still attached. The epidermis immediately dorsal to the attachment of the placodal ganglion has resumed its normal appearance, having a rough

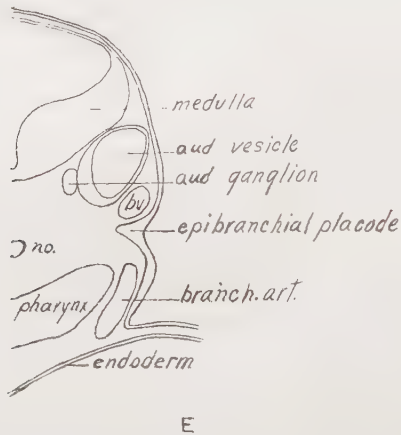


FIG. E. A camera tracing corresponding to fig. 56, showing the position of the epibranchial placode. NO. notochord; b.v. blood vessel.

inner border composed of cells which seem to be in process of becoming mesectoderm. Ventral to the placode the epidermis is still thick and the appearance here, as elsewhere in the formation of epibranchial placodes, indicates that the epidermis ventral to the ganglion is the chief source of whatever cells migrate into it.

The following section (fig. 56) presents approximately the same appearance except that the nuclei of the epidermis are separated from those of the ganglion which is attached to the epidermis by a cytoplasmic mass only. In fig. 57, however, we find the ganglionic mass detached from the ectoderm and lying free in the mesectoderm, while the epidermis resembles that of adjoining

regions. This portion of the ganglion was never attached to the epidermis at this point, but has grown backward and upward from the points indicated in the two preceding figures. The ganglion has now become longer than its point of attachment to the epidermis. Fig. 60, 93 hours, illustrates the first stage in which the epibranchial ganglion of the IXth is first completely detached from the epidermis. This section is taken through the point where the ganglion lies nearest the epidermis, *i.e.*, near the anterior border of the ganglion. Careful measurements of the length of the ganglion and of its point of attachment in a series of stages make it evident that the ganglion grows as indicated.

TABLE III

Showing the relative length of the epibranchial ganglion of the IXth as compared with the length of attachment (A. melas).

Age in hours.....	69	75	81	86	93	99	105	113
Length of attachment to placode in sections.....	3	2	2	2	0	2	1	0
Length of epibranchial ganglion in sections.....	3	7	12	12	19	25	13	15

In the first series (69 hours) the mesially projecting mass is no longer than the thickening, but in the following series the ganglion occupies seven sections and the attachment two. In the later stages the ganglion elongates rapidly up to 99 hours, where it is twenty-five sections in length, and after that, owing to its becoming placed in a dorso-ventral position, is not so long. In an embryo of 93 hours the ganglion is not in contact with the skin, but is found in contact in two later series, 99 and 105 hours, and after 113 hours it is permanently detached. The placode does not present the appearance of adding cells to the ganglion after the 93-hour series. The anterior end of the ganglion seems to be simply lying in contact with the epidermis which no longer resembles a placode. The epidermis has not yet resumed its normal appearance, but shortly after this stage there is nothing in the character of the epidermis to indicate the point at which the ganglion arose.

The introduction of the term 'branchial sense organ' by Frieriep and Beard seems unfortunate. Frieriep ('85) applied it to the epibranchial placodes of mammals, and Beard ('85-'86) to both epibranchial and dorso-lateral placodes apparently, and the term is used by Wilson ('91) in his paper on the sea bass. In all cases the term seems an unfortunate one. The epibranchial placodes of *Ameiurus* have no resemblance whatever to sense organs, particularly to gustatory organs, and the dorso-lateral placodes while resembling, in *Ameiurus*, lateral line organs do not give rise to lateral line organs. This is true in *Necturus*, as shown by Miss Platt ('95). The branchial sense organs of Wilson are apparently the dorso-lateral placodes. Whatever may have been the phylogenetic history of these placodes, it is much better to designate them in such a way as not to commit oneself to a theory as to their phylogenetic origin until it can be shown what that origin was. I have, therefore, followed von Kupffer ('94) and have used the term 'placode' exclusively. The distinction brought out (p. 56-57) in the discussion of the relation of the pre- and post-auditory placodes to the specific lateral line organs finds a striking parallel in the relations of the epibranchial placodes to their specific sense organs, the taste buds.

The lateral line organs arise in *Ameiurus* as definitely localized differentiations of the epidermis, and are not derived from the dorso-lateral placodes (pre- and postauditory placodes of *Ameiurus*), although they receive their innervation from ganglia derived from these placodes in the case of the X, IX and the VIII nerves.

The taste buds bear the same relation to the epibranchial placodes, as shown by the writer (Landacre '07). The taste buds appear simultaneously at the extreme anterior end of the oral cavity (ectoderm) and on the endoderm of the first three gill arches and spread posteriorly from the gills into the pharynx and œsophagus and from the anterior end of the oral cavity back into the mouth and externally over the lips, barbules and outer surface of the head and finally over the whole body.

The taste buds appear in well defined groups determined largely by the distribution of the rami of the nerves carrying gustatory fibres. These groups are isolated at first and later become con-

fluent and always appear in order from anterior to posterior. The taste buds show one other peculiarity in their order of appearance. They appear, generally, at the peripheral distribution of the nerves innervating them anterior to the ear, and in the reverse order posterior to the ear. It is evident from these facts that they are in no way, in *Ameiurus*, closely related in place of origin to the epibranchial placodes. The epibranchial placodes, so far as any evidence secured from their ontogeny indicates, are to be looked upon as ganglion forming structures. The epibranchial placodes bear no resemblance to either single taste buds or groups of taste buds. These buds spread in the case of the oral and superficial head buds from the point of origin toward, and not away from the point of origin of the placodes.

An additional fact of significance is the time intervening between the detachment of a given placode and the appearance of the first taste buds innervated by fibres derived from the ganglion formed by the placode. In the IXth nerve, the placode which forms the special visceral ganglion of that nerve becomes detached in a 93-hour embryo (*A. melas*), but the first taste buds on the pharynx, and, in fact, on any part of embryo, appear in a 113-hour embryo; a length of time sufficient to suggest that the appearance of the taste buds is associated with the appearance of the nerve trunk, rather than with the proximity of the taste buds to the placode, since the IXth nerve has a fibrillated root and trunk which extends into the first gill arch in an embryo on 113 hours.

The process of growth by which the various components of the peripheral nerves find their appropriate sense organs furnishes one of the most puzzling problems in embryology. This is especially true of the gustatory nerves and taste buds, and in a measure is true of the lateralis system of nerves and sense organs. The solution does not seem to lie in deriving both nerves and sense organs from a common primordium, as can be done in the case of the olfactory nerve and optic nerve. The distance between the point of origin of taste buds supplied by the VIIth nerve and the point of origin of the ganglion of the VIIth nerve precludes such an explanation. The suggestion offered above that there is some coördination in the growth of the peripheral fibres and the appear-

ance of the taste buds seems much more in accordance with the facts.

A good deal of interest attaches to the dorsal extension of the epibranchial ganglion. There is nothing in its composition or mode of development to indicate that it is formed otherwise than by the extension dorsally of the epibranchial placode. If, however, there are lateral mass cells in this ganglion they must enter into its composition at this point, and for this I find no evidence.

Herrick ('01) states that he finds no fibres derived from this ganglion except gustatory or special visceral, and since there is no evidence that cells other than those derived from the epibranchial placode enter into its composition we are driven to the conclusion that the epibranchial placode furnishes those cells which give rise to gustatory fibres and that those cells which give rise to general visceral fibres in the IXth ganglion of other species must come from the lateral mass or from the neural crest.

The evidence for the presence of general visceral fibres in the IXth nerve is exactly like the evidence for the presence of lateral mass cells in the ganglion. Neither has been detected. There is a possibility of both having been overlooked, of course, but if they should be found to be present it would not in my estimation affect the conclusion drawn. It would simply fall short of a demonstration. The fact that the VIIth, IXth and various portions of the Xth ganglia possess gustatory fibres approximately in proportion to the extent to which the epibranchial placodes contribute cells to these ganglia materially strengthens the conclusion. The geniculate ganglion of the VIIth has a well defined lateral mass contingent, as was shown in describing this ganglion. That portion of the visceral Xth from which arise the large visceral rami is almost exclusively derived from the lateral mass, containing only small contingents from the reduced fifth and sixth epibranchial placodes. The number of gustatory fibres derived from this ganglion is correspondingly small.

The third and fourth epibranchial ganglia possibly contain small constituents from the lateral mass. These ganglia, however,

are in such close proximity to the large lateral mass ganglion of the Xth that general visceral fibres might easily grow into the nerves, so that we cannot infer the presence of lateral mass cells simply because general visceral fibres may be in the peripheral nerves of these ganglia. The IXth is unique in that neither general visceral fibres nor lateral mass cells have been found in its composition.

Aside from the explanation given above, there seems to be no reason for the presence of the epibranchial placodes in the head, and for the part they play in contributing cells to those ganglia only which supply fibres to gustatory organs. The gustatory organs are all innervated from the cerebral ganglia, and only those cerebral ganglia give rise to gustatory fibres which contain cells derived from the epibranchial placodes, and the ganglion which seems to give rise to gustatory fibres only seems also to come only from the epibranchial placode.

My series at this stage are taken four hours apart, and the epibranchial ganglion acquires a connection with the proximal portion of the lateralis IXth (figs. 58 and 59) before losing its connection with the epidermis. However, the growing point of the epibranchial root is extremely thin. It passes up internal to the cardinal vein, which is in striking contrast with the growing parts of the epibranchial ganglia of the second and third true gills which pass up toward the brain external to the same vein (figs. 65, 66, 67, 68, and 69). The growing point of the IXth between the thicker portion derived from the epibranchial placode and the lateralis IXth, is shown in fig. 58. In the preceding series (75 hours) this connection is only one cell thick and in an embryo of 69 hours it is entirely absent.

THE ORIGIN OF THE LATERALIS IXth GANGLION

After reaching the level of the auditory vesicle in its dorsal extension, the growing point of the root of this epibranchial ganglion comes into contact with a mass of cells derived from the posterior and ventral portion of the auditory vesicle, which later forms the lateralis ganglion of the IXth. It is not derived from

nor directly related to the Xth, nor is it at first in contact with the auditory ganglion proper, but arises separately and can be followed continuously until it assumes the relations ascribed to it in the adult by Herrick ('01). At one stage in the enlargement of the auditory vesicle its relations are somewhat confused on account of the fact that the vesicle grows back and around the ganglion, but it can be followed, as mentioned, continuously. There is a later stage also where the lateralis IXth comes into contact with the motor root of the IXth and before the motor root has grown ventrally as far as the root of the epibranchial ganglion, when it is impossible to distinguish between the lateralis cells and the cells of the growing motor root. This condition is illustrated in fig. 59. In this stage we have the lateralis ganglion and the motor root closely combined. The constituents which can be positively identified as entering into the IXth ganglion are: first, the cells derived from the epibranchial placode situated in the distal portion of the ganglionic mass in the early stage, and extracranially in the latter stages: and secondly, the proximally situated lateralis ganglion, derived from the posterior portion of the auditory vesicle and closely associated with the motor root in its early stages, and in the later stages situated intracranially.

In discussing the differentiations of the postauditory lateral mass (p. 349-50) attention was called to the appearance in one series of a slight condensation of the lateral mass derivatives, in the region of the IXth ganglion just posterior to the auditory vesicle. This condensation appears in some series and not in others, so that one cannot be positive that no cells derived from the lateral mass enter into the proximal or lateralis portion of the IXth ganglion in its later stages. The early stages of the lateralis IXth are quite definite in origin and distinct in outline, and if lateral mass cells do enter into its composition they would be homologous to the preauditory lateral mass, and the ganglion would have a double composition and would resemble the VIIIth, if this ganglion contains lateral mass cells or the lateralis VIIth, rather than the lateralis Xth. The relations are difficult to unravel here, partly because of the presence of the motor root and partly because the cells

derived from the lateral mass are hard to distinguish from the surrounding mesectoderm. One can go no farther than to say that there is no well defined group of lateral mass cells entering into the lateralis IXth ganglion. The condition found in most of my series during the early proliferation of cells from the auditory vesicle before the definitive lateralis ganglion is formed, is illustrated in fig. 63. The lateralis IXth after it assumes a definite form is carried posteriorly by the backward growth of the auditory vesicle until it comes into the region of the slightly denser mass of mesectoderm, which at the time the lateralis IXth can first be detected is about seven sections posterior to the vesicle. This loose mass of cells, as mentioned above, is present in one of my series (*A. nebulosus*, Stage VII, figs. 40, 41, G), but in only one is it at all definite or does it present the appearance of an early stage of a ganglion. I take it to be the mass of cells which other authors have described as neural crest cells that enter into the IXth ganglion.

The early appearance of the definitive lateralis IXth ganglion is somewhat variable. It may not appear on both sides of the same embryo at the same time, and may vary in position, lying either on the ventro-mesial (fig. 61) or on the ventro-lateral side (fig. 62) of the posterior portion of the auditory vesicle. The definitive ganglionic mass may appear as a few loosely joined cells, some of which are still not entirely detached from the wall of the vesicle.

As in the case of the auditory ganglion, one can be quite sure that the bulk of the lateralis IXth ganglion is derived from the auditory vesicle. In the early stage of the vesicle there is no ganglionic mass in the position later occupied by the lateralis IXth, and the walls of the posterior end of the vesicle are clean cut and regular. Somewhat later the posterior wall becomes several cells thick, mitotic figures are numerous and a mass of cells is found attached to the ventro-mesial or ventro-lateral portion of the vesicle. No definite boundary can be determined for the forming ganglion, and cells are found in all positions between the wall of the vesicle and the body of the ganglion (fig. 63).

There is a well defined space, however, between the anterior end of the lateralis IXth and the posterior end of the auditory ganglion. The backward growth of the vesicle carries the ganglionic mass of the lateralis IX into the region occupied in some series by the condensation of the lateral mass, so that it is impossible to tell whether these lateral mass cells enter into the lateralis IXth or not. If they do, the lateralis IXth resembles the auditory rather than the lateralis Xth, which is derived solely from the postauditory placode.

Of the four acustico-lateralis ganglia in *Ameiurus*, the double ganglion belonging to the VIIth is derived solely from the lateral mass and shows its affinities with the general cutaneous Gasserian ganglion most closely, not only in the source from which it comes but in its mode of origin.

The lateralis Xth, derived from the postauditory placode, is decidedly unlike the lateralis VIIth, both in general appearance and mode of origin. It is from the early stages a well defined rod-like mass of cells whose long axis coincides with the long axis of the body, and is derived exclusively from the postauditory placode. Intermediate between these two extremes lie the auditory and lateralis IXth, which come largely if not exclusively from the auditory vesicle, but may have lateral mass cells in their composition.

The lateralis Xth is the most highly specialized of the four, and the reversal of the order of specialization, which usually proceeds from anterior to posterior, is at first sight striking. The whole acustico-lateralis system is, however, strictly a cranial specialization, the ganglia and nerves appearing first in the head and extending from there to the body, and having its center in the cranial region. The change from the generalized lateralis ganglion of the VIIth to the specialized lateralis ganglion of the Xth is in line with the order of appearance of the lateral line organs, which arise first in the cranial region, and later appear on the body. While usually a highly specialized structure lies anterior to a less specialized one, in the case of the acustico-lateralis ganglia the structure having a specialized mode of origin lies posterior to the one with a more generalized mode of origin.

THE ORIGIN OF THIRD AND FOURTH EPIBRANCHIAL PLACODES

The history of the first placode entering into the composition of the Xth ganglion, the third epibranchial, resembles very closely that of the epibranchial placode of the IXth ganglion, except that it forms its attachment to the brain in conjunction with the remaining roots of the Xth, by extending posteriorly until it joins the roots of the fourth placode. It can be detected first in my series (fig. 64) in a 69-hour embryo, at which stage it resembles very closely the early stage of the placode of the IXth nerve. In the next series (75 hours) the placode has proliferated quite a mass of cells mesially, but is not free from the epidermis at any point in its length, although three sections from its anterior end there is an evident constriction between the ganglionic mass and the epidermis.

In an 81-hour embryo the ganglion is not in contact with the epidermis at its posterior end, and has acquired a connection with the mass of cells lying over the site of the fourth and fifth epibranchial placodes of the Xth (fig. 79). In an 86-hour embryo the ganglion is still attached to the epidermis, but is somewhat larger and its root somewhat more evident. In a 93-hour embryo (figs. 80 and 65) the ganglion is still attached at its anterior end. In fig. 66, 93 hours, taken from a section following 65, the ganglion is attached by a very narrow neck of cells and throughout the remainder of its length is entirely free (figs. 67, 68, 69, 70) extending posteriorly into a narrow neck of cells which connects it with the last division of the Xth nerve. The root of this nerve, as mentioned above, lies lateral to the cardinal vein, as do all the other placodal roots of the Xth. The appearance of the epidermis near the placode resembles closely that in the region of the IXth. Anterior, dorsal and posterior to the placode the epidermis is usually one or two cells thick and quite ragged, presenting the appearance of proliferating cells into the mesectoderm. The thickening of the placode extends ventrally in the epidermis and, as in the case of the IXth, this region presents the appearance of furnishing most of the cells that move into the ganglion. Mitotic figures are occasional both in the epidermis and the placode.

There seems to be no question that here, just as in the case of the second placode, we have first a thickening of the epidermis above and behind the second true gill slit, followed by a proliferation of cells dorso-mesially to form the body and root of the ganglion, and later the complete detachment of the proliferated mass from the epidermis. The attachment disappears last at the extreme anterior end in an embryo of 99 hours. The dorsal extension of this placodal ganglion resembles closely the dorsal extension of the placodal ganglion of the IXth nerve; but the fact that it grows back parallel to the dorsal extension of the fourth epibranchial ganglion, and that both soon come into contact with the lateral mass ganglion of the Xth whose boundaries are at this stage not well defined and which is surrounded by mesectoderm make it more difficult than in the case of the IXth to determine whether there are lateral mass cells in its composition. General visceral fibres, if present in this ganglion, might be traceable either to lateral mass cells incorporated into the ganglion, or they might easily grow into it from the large lateral mass ganglion of the tenth, situated over the fourth and fifth gills. The conditions are by no means as favorable for drawing a definite conclusion as to the composition of the ganglion as in the case of the epibranchial ganglion of the IXth.

The development of the fourth epibranchial placode which gives rise to the fourth epibranchial ganglion resembles closely that of the second and third. In an embryo of 81 hours the posterior extension of the placodal ganglion has come into contact with the lateral mass ganglion situated just over the fourth gill slit at a point just ventral to that at which the root of the second epibranchial ganglion joins the same mass (fig. 79).

I have been unable to detect the placode in a 69-hour embryo. My 75-hour embryo is defective at this point. In the 81-hour embryo the ganglion is in contact with the epidermis throughout about half its length. The conditions are so similar here to those of the IXth, and first placode of the Xth, that I am sure that the method of appearance is the same. In fig. 68 (93 hours) is shown the appearance of the placode at the anterior portion of its attachment to the epidermis. Fig. 69 is taken two sections posterior

to 68 and shows the complete detachment of the posterior end of the ganglion from the epidermis. Fig. 70 shows the appearance of this ganglion seven sections posterior to the section from which fig. 69 was drawn, and just anterior to its union with the anterior portion of the lateral mass ganglion over the fourth gill slit. Fig. 71 shows the point of union of this ganglion with the anterior end of this lateral mass ganglion. The only difference between this placode and the third epibranchial lies in the thickness of its posterior portion, that part corresponding to the root of the third epibranchial ganglion. It lies much nearer its destination and apparently does not become so attenuated in reaching it. The later history of this ganglionic mass (figs. 81 and 82, *Ep. G. IV*) shows that it fuses much more closely with the ganglionic mass lying posterior to it than does the third, and may contain lateral mass cells, although I cannot be sure that they enter into its composition. It becomes completely detached from the epidermis in an embryo of 105 hours; while both the third and fourth epibranchial ganglia can be recognized in my oldest series, the fourth fuses much more closely with the remainder of the Xth than does the third.

THE ORIGIN OF THE FIFTH AND SIXTH EPIBRANCHIAL PLACODES

In the case of the fifth and sixth epibranchial placodes conditions are quite different on account of the fact that the lateral mass enters so prominently into the composition of this portion of the Xth. The relations are somewhat confused here on account of the enormous size of the lateral mass at the time the fifth and sixth placodes appear. The earliest trace of a placode I have been able to find for the fourth gill slit is represented in fig. 70 (93 hours). This placode has the appearance that all the other placodes present at the time they begin to proliferate cells mesially. The appearance usually presented in my preparations is shown in figs. 72 and 73. The large lateral mass ganglion comes into contact with the epidermis and remains in contact about the length of time the other placodes retain their connection with the epidermis. Except for the condition shown in fig. 70 it would not be possible to as-

sert that we had a true placode here. However, I believe that the contact of the lateral mass ganglion with the epidermis is purely a secondary matter and that while it cannot be proven, in all probability the fifth epibranchial placode is contributing cells to the lateral mass ganglion. I can see no other interpretation for the presence of the early stage of the placode before the contact, or the persistence of the contact during the time usually occupied in the proliferation of cells from the placode. As mentioned above, however, I have been unable to separate this ganglionic mass into lateral mass and placodal portions.

Fig. 72 is taken through the middle of the fifth epibranchial placode of a 99-hour embryo. The attachment of the lateral mass to the placode is here slightly anterior to the anterior end of the *lateralis Xth*, which does not appear in the figures. Fig. 73 is from an embryo of 105 hours. The *lateralis Xth* and lateral mass are cut through the anterior portions. The placodal thickening is seen to extend ventrally in the epidermis as do those of the second, third and fourth placodes. The attachment to the epidermis does not continue up to the 113-hour stage, and judging by the distance of the ganglion from the epidermis in this stage may disappear some time before this, perhaps between the 105 and 113-hour stages.

The sixth epibranchial placode is less prominent than the fifth. The lateral mass ganglion retains its contact a shorter time with the epidermis, which is slightly thickened, and I have not been able with certainty to identify the placode previous to the time the contact is formed. The series from which I describe it are taken from 6 to 8 hours apart, and this is not sufficiently close to be sure that the placode is not visible before the time of contact of the lateral mass with the ectoderm.

In an embryo of 113 hours there is present a second contact between the lateral mass cells and the epidermis. This contact occurs at the posterior end of the lateral mass portion of the *Xth* ganglion, which is quite large at this time and extends back of the fifth gill slit. The contact is present in an embryo of 113 hours from which fig. 74 was drawn, and must have been formed earlier but does not continue as long as the 120-hour stage. I have been

unable to determine to what extent cells move from the placode into the ganglion, since there seems to be no noticeable distinction between placodal cells and lateral mass cells in any of my embryos. The same reasoning applies here, however, that was used in the case of the fifth epibranchial placode. The location, time of appearance, and manner of thickening of the epidermis resemble the third and fourth placodes in their early stages when they are undoubtedly contributing cells to these ganglia. Its more transient character is in keeping with the reduction which has occurred in the fifth epibranchial ganglion as compared with the fourth, but seems more marked. It indicates a reduction of the placodes from posterior to anterior, and is to be associated with the reduction in the number of gills in the bony fishes as compared with cyclostomes and elasmobranchs.

The time at which the contact occurs and the length of the attachment of the IXth and the four epibranchial ganglia of the Xth is shown in the following table:

TABLE IV

Showing the time at which the epibranchial placodes of the ninth and tenth ganglia appear, the time at which they become detached, and the length of time of attachment.

EPIBRANCHIAL PLACODES	TIME OF FIRST APPEARANCE	TIME OF DETACHMENT	LENGTH OF TIME OF ATTACHMENT
	<i>hours</i>	<i>hours</i>	<i>hours</i>
Second.....	56½	93	37½
Third.....	69	99	30
Fourth.....	75	105	30
Fifth.....	93	-113	-20
Sixth.....	105+	113+	+8

This table shows that the fifth and sixth epibranchial placodes appear in serial order and become detached from the epidermis in the same order. They differ principally in having a shorter total time of attachment. There seems to be no reason for supposing that conditions are different here other than in the reduction of the placodes and in the presence of a well defined lateral mass ganglion which fuses with the placode.

The condition here seems to throw some light on the interpretation given these placodes by former workers. They have so often been described as arising at the time the neural crest ganglion fuses with the epidermis that I am unable to reconcile the conditions existing, under which the placodal ganglia of the IXth and first two divisions of the Xth arise in *Ameiurus*, with these descriptions, unless there are neural crest cells in the IXth and first two divisions of the Xth, which fuse with the epidermis in an early stage in these types. Until the nerve components have been thoroughly worked out in these types in which the neural crest ganglia have been described as entering into the IXth and first two anterior divisions of the Xth, so that we can be sure as to whether there are general visceral fibres in these nerves, it is useless to speculate as to either their mode of origin or composition. The presence of a neural crest in the region of the IXth and Xth nerves, however, does not prove the presence of neural crest cells in these ganglia, unless they can be definitely traced into them. The absence of a lateralis ganglion and fibres in the IXth nerve in *Menidia* (Herrick, '99) and apparently in *Gadus* (Herrick, '00, p. 296) and its presence in *Ameiurus* (Herrick, '01) indicate how useless it is to speculate as to the composition of these ganglia in one type because we know them in another which is closely related.

LATER HISTORY OF THE LATERAL MASS GANGLIA OF THE XTH

There are two of these ganglia in *Ameiurus*: (1) the small general cutaneous ganglion, the jugular, situated intra-cranially (Herrick, '01, p. 210). This ganglion is present in *Gadus* (Herrick, '00, p. 297), where it is also intra-cranial. In *Menidia*, however, the ganglion is small and wedged in between the visceral ganglia and is extra-cranial.

(2) Beside the jugular ganglion there is the large visceral ganglion situated extra-cranially over the fourth and fifth gill slits, the earlier history of which was taken up with the postauditory lateral mass. Some idea of its size at the time it comes into contact with the placodes of the fourth and fifth gill arches can be obtained from

fig. 73 which, however, is not taken through the largest portion of the ganglion. Herrick ('01) does not give a description of the communis ganglion of the Xth nerve in *Ameiurus* further than to call attention to the fact that it is typical, and in describing *Gadus* ('00) calls attention to the fact that it is similar to *Menidia*. In *Menidia* (Herrick, '99) the fifth branchial nerve is larger than the other four and gives rise not only to the fibres for the fifth gill arch but also to the fibres for the great visceral and oesophageal rami of the vagus. He also calls attention to the fact that in *Menidia* the ganglia of the glossopharyngeus and first branchial ganglia of the vagus are composed of very large cells with medium and small cells intermingled among them, and that as we go toward the caudal end of the ganglionic complex, while there are still found cells of various sizes, the smaller ones become increasingly numerous, and suggests the hypothesis that the larger cells are related to taste buds and the smaller ones to visceral fibres.

The division of the extra-cranial Xth ganglion into four parts can hardly be so distinct in *Ameiurus* as Herrick describes it in *Menidia*, since in my oldest series the last two divisions are not easy to distinguish and the fusion is probably much more marked in the adult. At the time the fifth and sixth placodes of the Xth nerve are present the lateral mass ganglion appears as a dense mass of cells lying over the fourth and fifth gill slits. The first two divisions of the Xth which are placodal in origin can be distinguished easily, and the first of these in any series is distinct up to a late stage.

We have here in the Xth nerve, then, a general cutaneous or jugular ganglion derived from the lateral mass and lying intracranially, and an extra-cranial visceral ganglion in which it is not possible to separate the placodal cells from the lateral mass cells which greatly predominate over the cells derived from the fifth and sixth epibranchial placodes. This whole ganglionic mass is described by Herrick as a communis ganglion. We must add to this large extra-cranial mass the two anterior placodal ganglia which however can be distinguished easily from the combined lateral mass and placodal portion. These relations are rendered clear by figs. 79, 80, 81, and 82.

The embryological evidence based on the mode of origin of the Xth ganglion strongly supports Herrick's suggestion, based on a study of the adult condition in *Menidia*, since the general and special visceral ganglionic cells come from two different sources although combined into one ganglionic mass.

The intra-cranial or jugular ganglion is the last of the cranial ganglia to assume definite form, and can be recognized first as a definitive ganglionic mass in an embryo of 113 hours. At this time the backward growth of the ear has carried the lateralis IXth quite near to the future jugular ganglion, but they are separated here as in all preceding stages by a blood vessel. Between the 69-hour stage and the 113-hour stage the jugular ganglion is not definitely formed and appears gradually as a mass of cells surrounding the root of the Xth nerve and extending from near the medulla down around the root of the nerve to the extra-cranial portion. Preceding the stage of 69 hours, and particularly before the formation of a fibrillated root, it is not possible to distinguish a definitive jugular ganglion from those cells which will form the extra-cranial portion. The history of the jugular ganglion seems to be briefly as follows: First there is a loose mass of cells extending from the brain ventrally to a point where the epi-branchial placodes will be formed (fig. 75). This is followed by a stage in which the visceral ganglion develops and the fibrillated root is present, and in which the jugular ganglion surrounds the root, sometimes thicker on one side, sometimes on the other, and extends down over the root to the enlarged extra-cranial portion. This is followed by a stage in which there is a definitive ganglionic mass present, which owing to the development of the cartilaginous skeleton can be designated as intra-cranial. This is connected with the extra-cranial portion by a mass of spindle shaped cells only, lying on and among the fibres of the root of the Xth nerve. These spindle shaped cells I interpret as sheath cells, so that the jugular ganglion is now quite distinct and can be easily differentiated from the extra-cranial communis ganglion after 113 hours in *Ameiurus*.

There is little change in the appearance of this ganglion until the stage of 81 hours, when the fibrous root of the Xth nerve is

present. The ganglion cells then surround the proximal part of the root as indicated in fig. 76, which is taken through the middle of the root and is not exactly transverse to the long axis of the embryo, so that nearly the whole length of the fibrous root shows. The cells occupying the proximal portion of the root where the definitive jugular ganglion appears surround the root, lying anterior and posterior to it.

There is little difference in size between the cells which occupy the position in which the ganglion is later found and those cells surrounding the future root. This condition persists for some time, but in an embryo of 113 hours there is a decided increase in the number and a change in the appearance of the cells as shown in fig. 77, which is taken through the middle of the root. Anterior and posterior to this point the cells are usually grouped on either side of the fibrous portion of the root.

A much later stage (fig. 78) from an embryo of 138 hours shows this ganglion after it has become a prominent portion of the vagus complex. The manner in which the ganglion cells are distributed through the root and their small size explains the difficulty one finds in separating the cells of the future ganglion from the spindle shaped cells of the root. The extra-cranial portion of the lateral mass I shall not describe further in detail. It is so large and increases in size so rapidly that it is by far the most conspicuous structure in this region of the body. It is too large, in fact, to draw under a camera at the same magnification I have used for the other portions of the ganglia. The figures (72 and 73) show it in the early stages and figs. 79, 80, 81 and 82 show its relative, size and relations. There is never any difficulty in locating the bulk of this ganglion after the 81st hour. There is the difficulty of determining its dorsal boundary, mentioned above, since it extends as a thin mass of cells dorsally to join the jugular. Its separation from the jugular is in all but these early stages, quite distinct.

The fact that this lateral mass ganglion consists of two parts, an intra-cranial which is general cutaneous, and an extra-cranial which is visceral supplying visceral surfaces, has an interesting bearing on the relation of spinal and cranial nerves.

The spinal ganglia derived from the neural crest furnish both general visceral and general cutaneous fibres, but these two components are combined in the same ganglion, although probably having separate terminations in the cord. In the head, however, we have the lateral mass ganglion of the Xth, which probably corresponds to the neural crest ganglion of other types, differentiated into two ganglia, a general cutaneous, the jugular, situated intracranially, and an extra-cranial portion that is in all probability the general visceral ganglion.

From the preceding description it will be seen that there are two quite distinct sources of origin for the cerebral ganglia in *Ameiurus*, the lateral mass and the epibranchial placodes. Unlike most types, there is no well defined neural crest. The lateral mass early gives rise to the dorso-lateral placodes represented by the auditory vesicle and the pre- and postauditory placodes, while the remainder of the lateral mass gives rise to the primordia of ganglia and to mesectoderm. The lateral mass doubtless contains beside the dorso-lateral placodes the homologue of the neural crest of other types, but the greater portion goes to form mesectoderm.

Of the components found in the adult ganglia, the special visceral or gustatory come from the epibranchial placodes, while the general visceral come from the ventral portion of the lateral mass. The general cutaneous component comes from the lateral mass also, but typically from the dorsal portion, as in the case of the jugular ganglion. The acustico-lateralis component shows its kinship to the general cutaneous component in that the lateralis ganglia of the VIIth come from the lateral mass. The auditory and lateralis IXth come chiefly from the auditory vesicle but may have lateral mass cells in their composition. They show a somewhat more specialized mode of origin, while the lateralis Xth comes entirely from the postauditory placode and is the most highly specialized in mode of origin of the acustico-lateralis ganglia. The geniculate ganglion was seen to be composed of constituents from both the ventral portion of the lateral mass and from the epibranchial placodes.

The visceral ganglion of the IXth nerve seems to be a pure placodal ganglion. The first two epibranchial ganglia of the Xth resemble the IXth, but may possibly contain lateral mass cells. The last two epibranchial ganglia of the Xth are quite small and combine with the large lateral mass portion so that the posterior portion of the visceral Xth is largely lateral mass in origin. These relations are shown in table V:

TABLE V

*Showing the source of the various components of the cranial ganglia of Ameiurus.
The presence of any given component is indicated by the word present.*

DERIVATION	V	VII	VIII	IX	X	X	X	X	COMPONENT
Lateral Mass	Dorsal portion	Pres-ent					Pres-ent	Pres-ent	General cutaneous
		Pres-ent	?	?					Acustico-lateralis
	Dorso-lateral placodes		Pres-ent	Pres-ent			Pres-ent	Pres-ent	Acustico-lateralis
	Ventral portion		Pres-ent		?	?	Pres-ent	Pres-ent	General visceral
Epi-branchial placodes		Pres-ent		Pres-ent	Pres-ent	Pres-ent	Pres-ent	Pres-ent	Special visceral

In this table the general cutaneous, general visceral and acustico-lateralis portions of the Xth are placed over the last two epibranchial ganglia not so much to indicate their segmental position as because they occupy this relative position. The lateralis Xth extends however much posterior to the visceral portion.

A comparison of this table with table II compiled from Herrick's work on *Ameiurus* (p. 321) shows that the ganglia are as discrete in their mode of origin as are the components of the adult ganglia

and nerves, with the single exception that we have portions of the acustico-lateralis ganglia, as shown in other types, arising from the same source as the general cutaneous. This is to be explained on the basis of the relationship of the two components. In sharp contrast with this, however, we have distinct sources of origin for the special and the general visceral ganglia which are combined in the preceding table (II) and which in the adult are closely fused, particularly in the geniculate and in the posterior portion of the tenth.

The differences between the two tables may be summarized briefly as follows: The visceral ganglia of the adult in table II (p. 321) are broken down in the table V into those portions derived from the epibranchial placodes, *i.e.*, the special visceral or gustatory ganglia, and the portions derived from the lateral mass, *i.e.*, the general visceral.

The acoustico-lateralis ganglia of the adult in table II are broken down in table V into those portions derived from the lateral mass, *i.e.*, the lateralis VIIth and possibly portions of the VIIIth ganglion and of the lateralis IXth, and those portions derived secondarily from the auditory vesicle and placodes, *i.e.*, all of the lateralis Xth and most if not all of the auditory and lateralis IXth ganglia.

GENERAL SUMMARY

1. The neural plate in *Ameiurus* differentiates longitudinally into three regions: a median region, the neural keel, which later becomes the neural tube, and two lateral regions, the lateral masses, separated from the neural keel by constricted areas.

2. After the body has assumed a rounded form, the lateral masses come to lie on the sides of the body still retaining their connection with the neural cord by constricted areas. Part of the lateral mass on either side differentiates into the auditory vesicle and the pre- and postauditory placodes, which are extensions of the vesicle and resemble it in structure. These represent the dorso-lateral placodes of other authors. The remainder of the lateral mass breaks down more or less completely into loose tissue in

which the general cutaneous, general visceral and some of the acustico-lateralis ganglia form, the remainder not thus used going to form mesectoderm. In the auditory region all of the lateral mass is converted into the auditory vesicle.

3. The Gasserian ganglion arises near the anterior end of the lateral mass, over the mandibular bar, and is first recognizable as a slightly denser area on either side of which the lateral mass breaks down into mesectoderm. Just posterior to this region the ventral portion of the lateral mass, over the hyoid bar, gives rise to part of the geniculate ganglion which later combines with the portion derived from the epibranchial placode, the two constituents not being separable shortly after fusion.

4. Just anterior to the auditory vesicle a portion of the lateral mass gives rise to the lateralis VIIth ganglia which does not differentiate into the dorso-lateral and ventro-mesial ganglia until later. The posterior end of this ganglionic mass is in contact with the auditory vesicle. Both the Gasserian and lateralis VIIth, and that portion of the geniculate derived from the lateral mass are, at first, small and ill defined, with irregular borders which pass almost imperceptibly into mesectoderm. Between the regions in which these ganglia appear the lateral mass breaks down into mesectoderm.

5. The auditory ganglion arises chiefly, if not exclusively, by the proliferation of cells from the anterior end of the auditory vesicle, but in such close contact with the preauditory lateral mass that one cannot be certain that there are no lateral mass cells in it.

6. The lateralis ganglion of the IXth nerve arises also chiefly, if not entirely, by proliferation of cells from the posterior end of the auditory vesicle, but it is carried by the backward growth of the vesicle into the region of the root of the IXth nerve, where a slight condensation of lateral mass cells is sometimes present, and it may possibly contain lateral mass cells.

7. Between the IXth and Xth ganglia and for some distance posterior to the anterior end of the Xth, the lateral mass breaks down completely into mesectoderm. In the region of the Xth nerve the dorsal portion of the lateral mass breaks down into

loose tissue, in which the general cutaneous jugular ganglion later appears, while the ventral region which forms the general visceral portion of the Xth retains its continuity to a greater extent. The ventral region of the lateral mass which enters into the Xth ganglion resembles in appearance and corresponds in position to that portion of the preauditory lateral mass which enters into the geniculate ganglion.

8. The preauditory placode which is the anterior continuation of the auditory vesicle extends as far forward as the hyoid gill slit, but between the ear and the hyoid gill slit it breaks down completely into mesectoderm. Its anterior extension disappears at the exact point where the epibranchial placode of the hyoid arch appears but seems to have no direct relation to it other than in its position. The preauditory placode does not give rise to the preauditory lateral line organs, there being a period of some hours between the disappearance of the placode and the appearance of the first lateral line organs.

9. The postauditory placode, which is the posterior extension of the auditory vesicle, becomes detached from the vesicle and moves back by successive differentiations of the epidermis to a point back of the fourth lateral line organ, where it gradually disappears. Before its disappearance there have appeared four lateral line organs anterior to it and at least two posterior to it. It disappears in the region of the fifth, but probably does not give rise even to that. The lateralis Xth ganglion arises by the proliferation of cells from the postauditory placode after it has moved some distance back of the auditory vesicle. After the placode ceases to contribute cells to the ganglion it moves beyond the posterior limit of the ganglion, losing all connection with it, and does not give rise to the lateral line nerve.

10. Both the pre- and postauditory lateral line organs are formed by gradual differentiations of the deeper layer of the epidermis, sometimes singly, sometimes two from a common primordium and are entirely distinct in origin from the placodes.

11. The epibranchial ganglia all have a common mode of origin. The epibranchial placode of the hyoid arch appears first as a thickening of the epidermis dorsal and slightly posterior

to the point of contact of the endodermal pocket of the hyoid gill slit with the epidermis. This thickening is characterized by the irregular arrangement of its nuclei and by the large number of mitotic figures. The thickening of the epidermis is followed by an active proliferation of cells mesially, which come into contact with the ventral portion of the lateral mass in this region. The proliferated mass later becomes detached and after some hours the geniculate ganglion, which is thus composed of a lateral mass contingent and a placodal contingent, assumes definite form and comes into intimate relation with the Gasserian ganglion.

12. The epibranchial placode of the first true gill slit arises in a similar manner, appearing first as a slight thickening lying dorsal and posterior to the first gill slit. The thickening is accompanied by active mitosis, proliferation of cells, and finally by complete detachment, *en masse*, of the proliferated cells. The proliferated epibranchial ganglion is in this case, however, apparently a pure placodal ganglion, since no lateral mass cells could be detected entering into its composition. Its dorsal extension comes into contact with the remainder of the IXth before the ganglion is completely detached from the epidermis however.

13. The epibranchial ganglia of the second and third gill arches have exactly similar modes of origin, but their dorsal extensions soon come into contact with the lateral mass portion of the Xth. While the second and third epibranchial ganglia are definite in outline and mode of origin, their proximity to the Xth makes it difficult to be sure that there may not be lateral mass cells in their composition.

14. The epibranchial ganglion of the fourth and fifth true gills, owing to the fact that they are in the region of the large lateral mass ganglion of the Xth, present a somewhat different history. The fourth can be detected before the lateral mass of the Xth comes into contact with it, and while its early stages resemble those anterior to it, it does not become detached before the fusion occurs between it and the lateral mass portion. In the case of the fifth, the epibranchial ganglion cannot be detected in my series before the fusion, so that while there is every reason for thinking that the fifth and sixth epibranchial placodes contribute cells

to the Xth, the relative amount cannot be determined and the two components cannot be separated. The visceral ganglia of the second and third gill arches are apparently like the IXth, pure placodal ganglia with possibly a small contingent of lateral mass cells, while the remainder of the tenth is composed of a few placodal cells derived from the small fifth and sixth epibranchial placodes united to a large lateral mass contingent.

15. The ganglia described in this paper as general cutaneous, acustico-lateralis, and visceral, have been followed to a late stage and shown to be the ganglia described by the authors under these names. The evidence from *Ameiurus* is little short of a demonstration that there are separate origins for the general visceral and for the special visceral systems, the former coming from the ventral portion of the lateral mass, or, in other types, from the neural crest, and the latter from the epibranchial placodes. For the acustico-lateralis system, there are two sources of origin. The lateralis VIIth comes entirely from the lateral mass and in other types apparently from the neural crest. The auditory and the lateralis IXth come chiefly from the auditory vesicle but may contain lateral mass cells, while the lateralis Xth comes entirely from the postauditory placode. The description of the acustico-lateralis system as a special cutaneous system finds a strong support in embryological evidence. The lateralis VIIth ganglia represent an intermediate stage between the general cutaneous ganglia, and the acustico-lateralis ganglia of the IXth and Xth nerves, resembling the former in mode of origin and the latter in structure and function. The latter are derived from the dorso-lateral placodes represented by the auditory vesicle and postauditory placodes. The general cutaneous ganglia of the Vth and Xth come from the dorsal portion of the lateral mass also, or neural crest of other types.

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ABBREVIATIONS

- | | |
|--|--|
| Au. G., Auditory ganglion. | Ep., Epidermis. |
| Au. G., I and II. First and second divisions of the auditory ganglion. | Ep. Pl. I, First epibranchial placode (epibranchial placode of the VII nerve). |
| Au. Ves., Auditory vesicle. | |
| Br. I, II, III, IV, V, First to fifth branchial nerves. | Ep. Pl. II, Second epibranchial placode (epibranchial placode of the IX nerve). |
| En., Endoderm. | |
| D. L. VII, Dorso-lateral portion of the lateralis VII ganglion. | Ep. Pl. III, Third epibranchial placode (first epibranchial placode of the X nerve). |
| D. L. M., Dorso-lateral mass. | |

- Ep. Pl. IV, Fourth epibranchial placode (second epibranchial placode of the X nerve).
- Ep. Pl. V, Fifth epibranchial placode (third epibranchial placode of the X nerve).
- Ep. Pl. VI, Sixth epibranchial placode (fourth epibranchial placode of the X nerve).
- Ep. G. II, Second epibranchial ganglion (epibranchial ganglion of the IX nerve).
- Ep. G. III, Third epibranchial ganglion (first epibranchial ganglion of the X nerve).
- Ep. G. IV, Fourth epibranchial ganglion (second epibranchial ganglion of the X nerve).
- G., Remnant of the lateral mass in the region of the lateralis IX ganglion.
- Gass. G., Gasserian ganglion.
- Gen. Com. X., General communis or visceral ganglion of the X nerve.
- Gen. G., Geniculate ganglion.
- J. G. X, Jugular or general cutaneous ganglion of the X nerve.
- L. IX, Lateralis ganglion of the IX nerve.
- L. G. X, Lateralis ganglion of the X nerve.
- L. L. X, Lateral line nerve trunk of the lateralis X ganglion.
- L. M., Lateral mass.
- L. M. G. VII, Lateral mass ganglion (general visceral ganglion) of the geniculate.
- Med., Medulla oblongata.
- Mes., Mesoderm.
- Mesec., Mesectoderm.
- N. C., Neural canal.
- Post Pl., Postauditory placode.
- Pre. Pl., Preauditory placode.
- R. X, Root of the X nerve.
- R. Au., Root of the auditory nerve.
- R. C. D. X., Ramus cutaneus dorsalis vagi.
- R. D. L., VII, Root of the dorso-lateral portion of the lateralis VII ganglion.
- R. Gass., Root of the Gasserian ganglion.
- R. Gen., Root of the geniculate ganglion.
- R. L. G. X, Lateralis root of the X nerve.
- R. S. J, Ramus supra-temporalis J, glossopharyngei, (Herrick, '01).
- R. V. L., VII, Root of the ventrolateral portion of the lateralis VII ganglion.
- R. A. A., Ramulus acusticus ampulæ anterioris.
- R. A. E., Ramulus acusticus ampullæ extrenæ.
- R. L., Ramulus acusticus lagenæ.
- R. N., Ramulus acusticus neglectus.
- R. P., Ramulus acusticus ampullæ posterioris.
- R. Sac., Ramulus acusticus sacculi.
- R. N., Ramulus acusticus recessus utriculi.
- T. Gass., Trunk of the Gasserian ganglion (supero-lateral strand of Wright).
- T. Gen., Trunk of the geniculate ganglion of the VII nerve (infero-mesial strand of Wright).
- T. V. L. VII, Trunk of the ventrolateral portion of the lateralis VII ganglion (hyomandibular nerve).
- V. L. VII, Ventrolateral portion of the lateralis VII ganglion.
- X, Mass of cells of unknown origin and whose fate is unknown, lying just anterior to the first epibranchial placode.
- V. L. VII, Ventrolateral portion of the lateralis VII ganglion.
- X, Mass of cells of unknown origin and whose fate is unknown, lying just anterior to the first epibranchial placode.
- Y, Ventral portion of the lateral mass lying in the region of the IX and X ganglia.

EXPLANATION OF FIGURES

All sections are cut 7 micra in thickness, and all figures and reconstructions are taken from transverse sections. Figures were drawn with a camera lucida with objective 4 mm. eye-piece, $\times 8$ Spencer, reduction to $\frac{1}{2}$. Total magnification, 186 dia.

1 (A. neb., Stage I) is taken at a stage when the medullary plate is slightly differentiated into the neural cord (N. C.) and the lateral mass (L. M.). The section lies just posterior to the point of formation of the optic cup.

2 and 3 (A. neb.) are taken from the same embryo, Stage II. Fig. 2 is taken six sections posterior to the optic vesicle and lies in a region just anterior to the point at which the Gasserian ganglion will form later. The lateral mass here breaks down completely into mesectoderm.

3 is taken just posterior to the future position of the Gasserian ganglion, twenty-nine sections posterior to the optic vesicle. The greater portion of the lateral mass here breaks down into mesectoderm also.

4 to 9 (A. neb., Stage III) are all from the same embryo which is slightly older than that from which figs. 2 and 3 were taken. Fig. 4 lies four sections anterior to the auditory vesicle and shows the differentiation of the lateral mass into the preauditory placode and the dorsal portion of the lateral mass which later forms the lateralis VII ganglion.

5 shows the differentiation of the lateral mass into dorso-lateral mass and post-auditory placode, four sections posterior to the auditory vesicle.

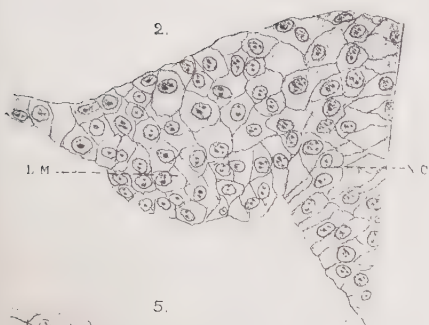
6 is taken through the middle of the auditory vesicle before the appearance of a definite cavity.

7 lies four sections posterior to the optic vesicle. It is taken through the same relative position as fig. 2, Stage I, and shows the transition of lateral mass into mesectoderm.

8 is taken through the region in which the Gasserian ganglion forms. The lateral mass does not break down into a loose mass of cells so early here as it does just anterior and posterior to the Gasserian ganglion.

9 lies five sections anterior to fig. 4 and nine sections anterior to auditory vesicle. It shows the reduction in size of the preauditory placode as one reads forward from the position of fig. 4.

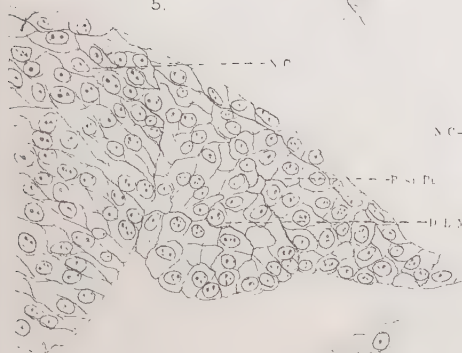
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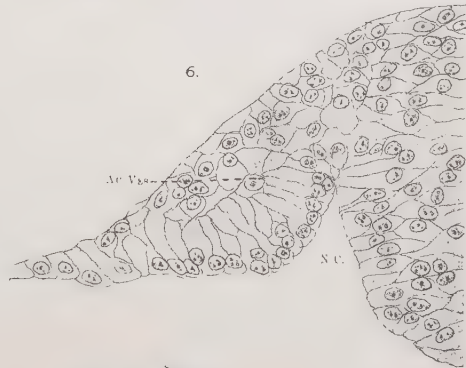
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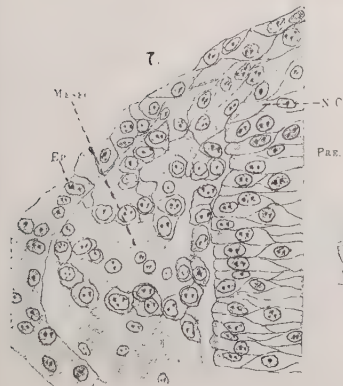
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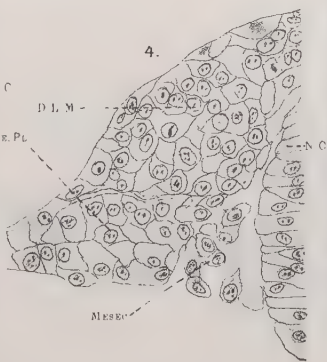
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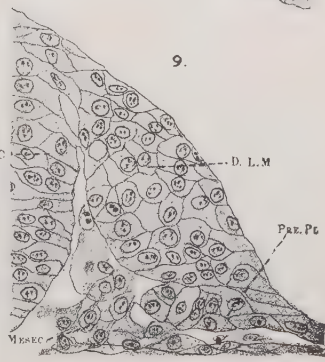
7.



4.



9.



EXPLANATION OF FIGURES

10 and 11 (A. neb., Stage V) are from the same embryo. Fig. 10 is taken through the posterior end of the Gasserian ganglion at one of the earliest stages at which it can be definitely located. This section passes through the hyoid gill pocket (En.).

11 is taken through the posterior end of the lateralis VII ganglion and lies four sections anterior to the auditory vesicle.

12 (A. neb., Stage VII) is from an older embryo than that from which fig. 6 was taken. It lies in the mid-region of the vesicle and shows the absence of a lateral mass after the vesicle is formed.

13 is taken from the same embryo as that from which figs. 10 and 11 were taken (A. neb., Stage V). It lies four sections back of the anterior end of the auditory vesicle. The proliferation of the capsule cells to form the auditory ganglion is taking place here.

14 and 15 (A. neb., Stage IV) are from embryos of the same age. Fig. 14 lies two sections anterior to the anterior end of the auditory vesicle. The preauditory placode is here continuous with the vesicle; on the opposite side of the same embryo there is one section, fig. 15, intervening between the preauditory placode and the vesicle.

16 (A. neb., Stage IV) is from a slightly more developed embryo of the same age as figs. 14 and 15 and is taken through the middle of the preauditory placode. There are six sections in which the placode is absent between the posterior end of the placode and the anterior end of the vesicle.

17 (A. neb., Stage V) is taken from an older embryo than the one from which fig. 16 is taken and lies nineteen sections anterior to the vesicle. The placode is here disintegrating and is entirely absent in the remaining eighteen sections. It is intact anterior to this point.

18 from the same embryo as fig. 17 shows the appearance of the preauditory placode at the posterior third of its contact with the hyoid gill pocket which extends over eleven sections. This is the last recognizable stage of the placode. It still retains a slight resemblance to the earlier stages.

19 to 24 (A. neb., Stage VI) are all from the same embryo. Fig. 19 is taken through the mid region of the hyoid gill pocket and shows the complete disappearance of the preauditory placode.

20, 21, 22 and 23 are consecutive sections, fig. 20 lying at the extreme posterior end of the point of contact of the hyoid pocket with the epidermis. The small mass of cells (X) lies anterior to the position of the future epibranchial ganglion and does not seem to enter into its composition. These sections show the gradual thickening and irregular arrangement of the cells in the epidermis (epibranchial placode) which precedes the proliferation of cells mesially.



EXPLANATION OF FIGURES

24 lies four sections back of fig. 23, the epidermis is reduced in thickness and the placode is not so long dorso-ventrally. Just back of this the epidermis is of normal thickness.

25 to 30 (A. neb., Stage VII), illustrating the origin of the epibranchial portion of the geniculate ganglion, are all from the same embryo which is slightly older than the one from which figs. 19 to 24 were taken. Figs. 25 to 28 are consecutive. Figs. 29 and 30 are consecutive, one section intervenes between figs. 28 and 29. Fig. 25 lies near the posterior limit of the contact of the hyoid pocket with the epidermis and fig. 26 at the extreme posterior limit. Active cell division is taking place here. In fig. 27 the ganglionic mass is proliferated mesially over the hyoid pocket which is no longer in contact with the epidermis. In fig. 28 the ganglionic mass is still purely placodal in origin, but in fig. 29 the placodal ganglion is in contact with a slightly delimited mass (L. M. G. VII) derived from the lateral mass. In fig. 30 the lateral mass portion of the ganglion predominates. A few sections posterior to this point the ganglion is entirely of lateral mass origin and the epidermis is of normal thickness.

31 to 39 (A. melas, 86 hours) illustrate the relations of the Gasserian ganglion to the geniculate and the dorso-lateral and ventro-lateral lateralis ganglia of the VII nerve. Figs. 37, 38 and 39 also show this relation to the auditory ganglion and vesicle. Preceding the stage of 86 hours it is not possible to differentiate between the two lateralis ganglia of the VII nerve and following this stage the ganglia soon becomes condensed and it is difficult to unravel them.

31 is taken through the trunk of the nerve (supero-lateral strand of Wright) of the Gasserian ganglion.

32 is taken just anterior to the point of origin of the nerve (infero-mesial strand of Wright) of the geniculate ganglion. These two strands combine in a later stage some distance from the ganglia and then split into the maxillary and mandibular nerves.

33 is taken through the root of the Gasserian ganglion.

EXPLANATION OF FIGURES

34 is taken through the anterior end of the dorso-lateral lateralis VII ganglion and the root of the Gasserian.

35 is taken through the trunk (hyomandibular nerve) of the ventral lateralis ganglion of the VII and the root of the geniculate ganglion.

36 is taken through the root of the ventral lateralis ganglion.

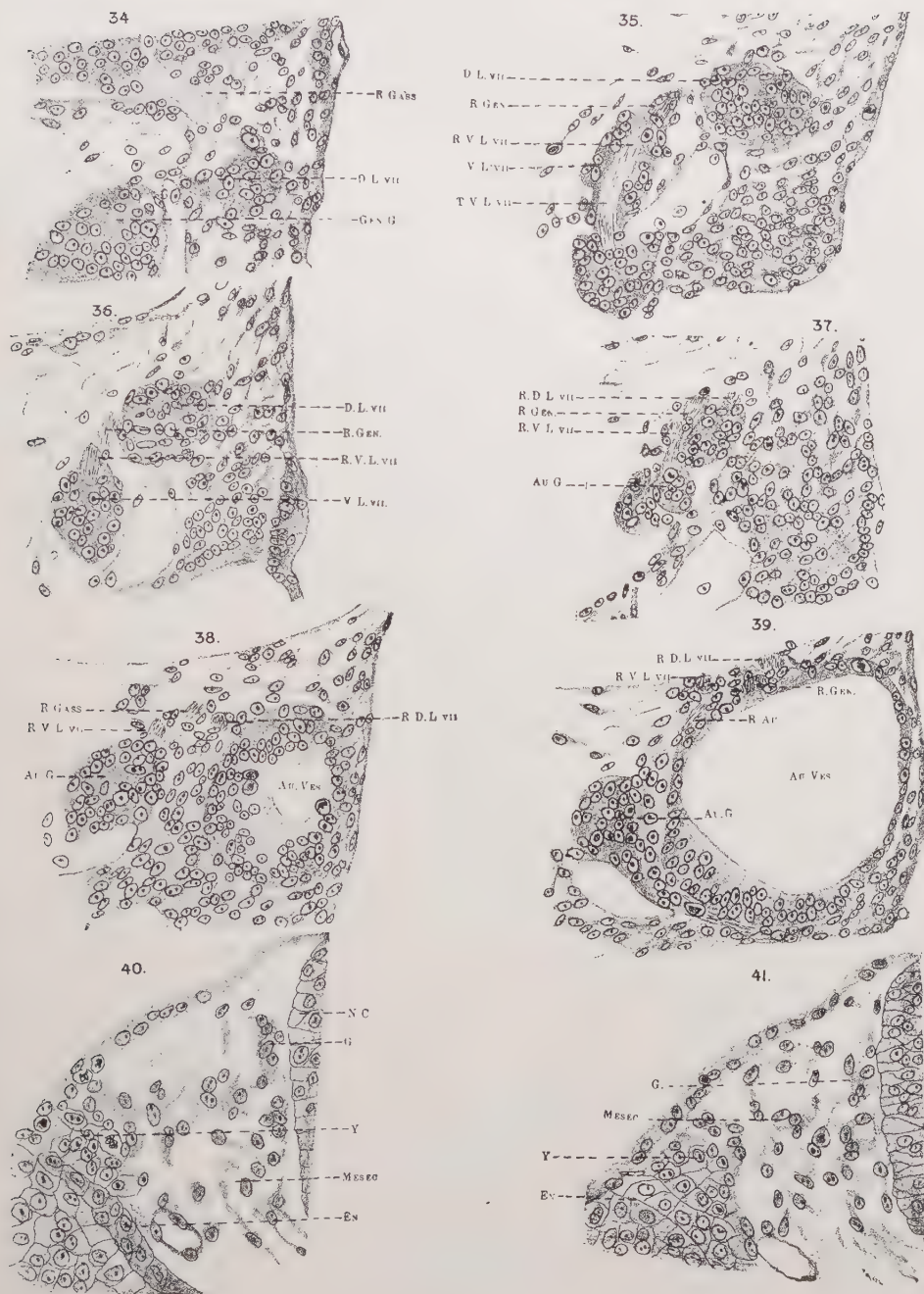
37 is taken through the extreme anterior tip of the auditory ganglion. The dorsal lateralis VII runs through figs. 34 to 37.

38 and 39 are taken through the anterior and median portions of the auditory ganglion. The roots of the dorso-lateral, ventro-lateral and geniculate ganglia appear in figs. 37, 38 and 39.

40 to 43 (A. neb., Stage VII) are taken from the same embryo as figs. 25 to 30. Figs. 40 and 41 are consecutive sections and show the only recognizable trace of a condensation of the cells derived from the lateral mass in the region of the IX nerve, except the ventral portion of the lateral mass (Y) which does not enter into the IX ganglion.

40 is taken one section posterior to the auditory vesicle.

41 is taken two sections posterior to the auditory vesicle.



EXPLANATION OF FIGURES

42 is taken five sections posterior to the auditory vesicle and lies just back of the point where the root of the IX later appears. The lateral mass is here completely converted into mesectoderm except the ventral portion (Y).

43 is taken through a condensation of lateral mass cells at the point where the root of the X and the jugular ganglion later appear. This mass cannot be located in later series for some time.

44 to 52 illustrate the detachment of the postauditory placode from the auditory vesicle, its migration and the formation of the lateralis X ganglion.

44 and 45 (A. neb., Stage IV) are consecutive sections. Fig. 44 being taken just at the point where the auditory vesicle passes into the placode by the disappearance of the dorsal half of the vesicle. Fig. 45 being near the anterior end of the placode, three sections posterior to the auditory vesicle.

46 is taken three sections posterior to the auditory vesicle and is from a slightly less developed embryo of the same age as figs 44 and 45. The vesicle passes gradually into the placode in this series.

47 to 51 (A. neb., Stage VII) show the characteristic appearance of the lateralis X ganglion as it is proliferated from the placode before the placode has moved beyond the posterior limit of the ganglion. Fig. 47 is twenty sections posterior to the vesicle; fig. 48 twenty-three sections; fig. 49 twenty-five sections; fig. 50 twenty-seven sections; and fig. 51 twenty-nine sections posterior to the auditory vesicle. Fig. 50 is at the extreme posterior limit of the lat. X ganglion.

52 (A. neb., Stage IX) shows the usual appearance of the lateralis X ganglion in a somewhat older series.

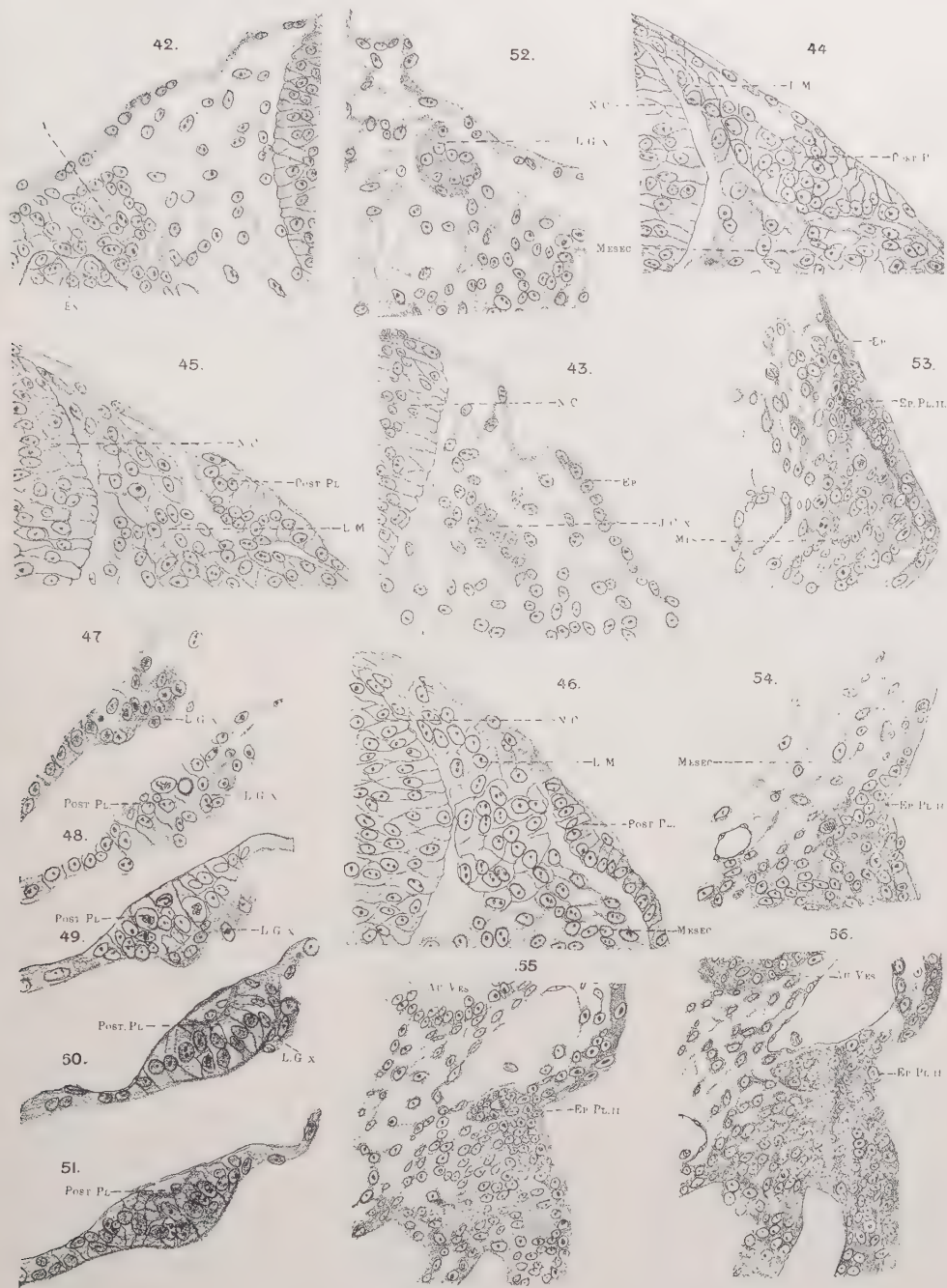
53 to 60 (A. melas) illustrate the formation and detachment of the epibranchial placode of the IX ganglion.

53 (A. melas, 56½ hours) shows the appearance of the placode when it can first be detected.

54 (A. melas, 69 hours) shows the extent of the thickening of the placode while the whole placode is still in contact with the epidermis.

55 to 59 are from the same embryo (A. melas, 81 hours) at a stage when the posterior end of the placode is detached from the epidermis and has formed an attachment to the root of the IX nerve which contains motor fibers and lateralis ganglion cells.

55, 56 and 57 are consecutive. Figs. 55 and 56 show the appearance of the ganglionic mass just before it becomes completely detached. The anterior end of the ganglion is attached, for some time after the posterior end is free, apparently by the growth dorsally and mesially of the ganglionic mass.



EXPLANATION OF FIGURES

57 is taken one section posterior to fig. 56 at the point where the ganglionic mass is free from the epidermis.

58 and 59 are taken through the root of the epibranchial ganglion of the IXth just before it comes into contact with the lateralis and motor portions of the IX, as shown in fig. 59.

60 (*A. melas*, 93 hours) is taken through the epibranchial ganglion at the nearest point of approach to the epidermis. This is the first stage in which the ganglion is completely detached from the epidermis. Its clean cut boundaries during all of its development indicate that no other cells than those derived from the placode are incorporated in the ganglion.

61, 62 and 63 (*A. neb.*) illustrate three stages in the formation of the lateralis IX ganglion of which fig. 63 (*A. neb.*, Stage V) is the earliest. The ganglion varies a great deal in appearance and somewhat in position. Fig. 62 (*A. neb.*, Stage IX) is older than fig. 61 (*A. neb.*, Stage VIII). Fig. 63, while taken from the posterior end of the vesicle, differs totally from the appearance of this region before and after the formation of the ganglion.

64 to 71 show the formation of the first two epibranchial ganglia of the X.

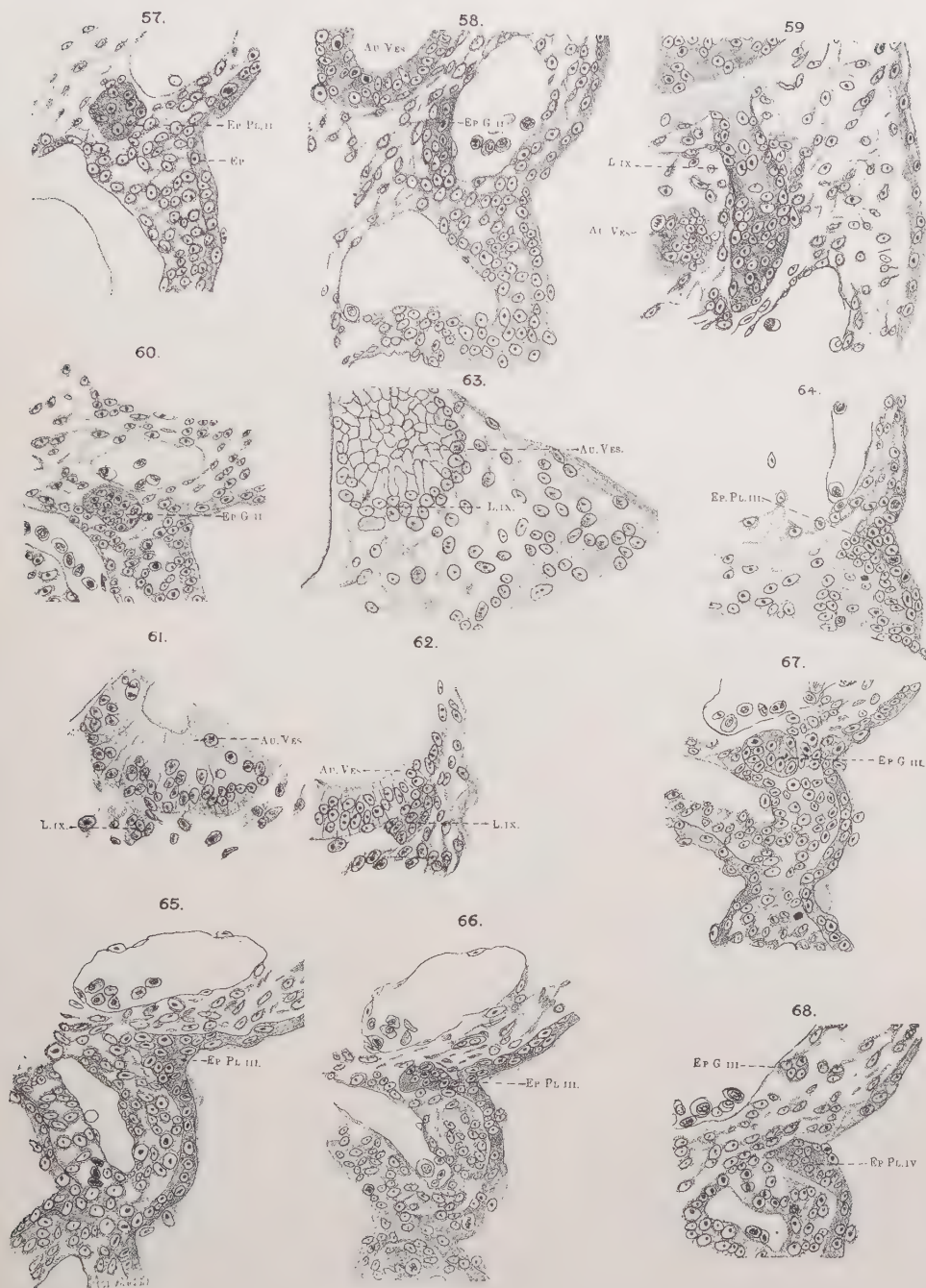
64 (*A. melas*) 69 hours shows the earliest recognizable trace of the third epibranchial placode. Figs. 65 to 71 are from the same embryo (*A. melas*, 93 hours).

65 is through the anterior portion of the placode.

66 is through the middle region just before the detached portion is reached.

67 is just back of the point of detachment.

68 is through the root of the third epibranchial ganglion and the fourth epibranchial placode. This probably is not the earliest trace of the fourth epibranchial placode, however. The preceding series is defective at this point.



EXPLANATION OF FIGURES

69 (*A. melas*, 93 hours) is taken through the detached portion of epibranchial ganglion IV, also shows the root of epibranchial ganglion III.

70 (*A. melas*, 93 hours) is taken through the fourth epibranchial ganglion just before it comes into contact with the lateral mass ganglion of the X (general communis X). In fig. 70 the root of the third epibranchial ganglion has become so attenuated that it cannot be recognized with certainty, although the two cells marked Ep. gl. III appear to be the posterior extension of this ganglion.

71 (*A. melas*, 93 hours) shows the point of union of the fourth epibranchial ganglion with the lateral mass of the X (Gen. vis. X).

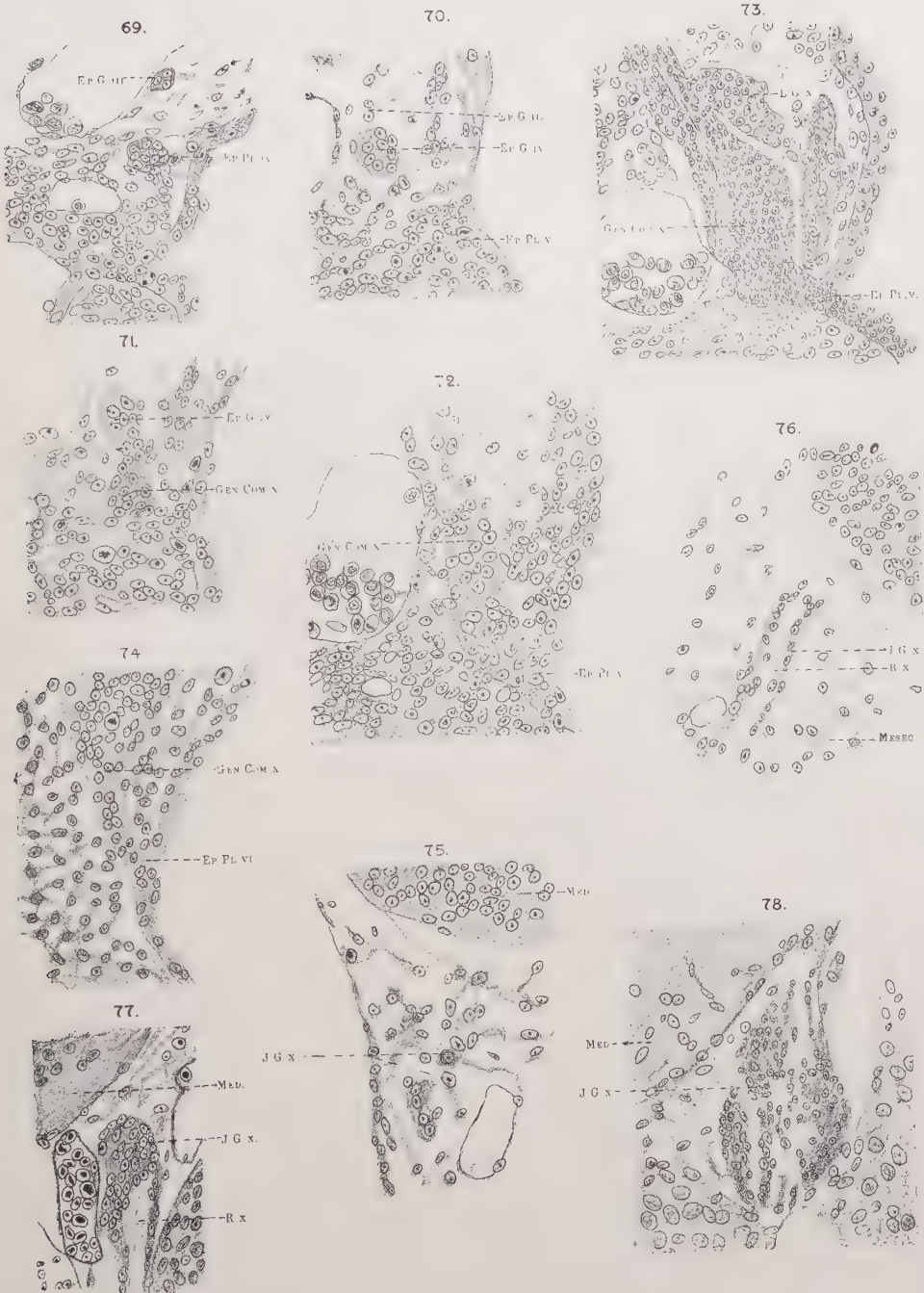
70, 72, 73 and 74 illustrate the conditions under which the fifth and sixth epibranchial placodes arise. In fig. 70 (*A. melas*, 93 hours) the fifth epibranchial placode appears before the lateral mass ganglion of the X comes into contact with the epidermis. In fig. 72 (*A. melas*, 99 hours) the attachment is quite like that in fig. 73 (*A. melas* 105 hours). In both these cases the attachment of a lateral mass (neural crest) ganglion to the epidermis is quite evident and corresponds to the oft repeated descriptions in the literature of the contact formed between neural crest ganglia and the epidermis. Nothing resembling this occurs in *Ameiurus* except in the fifth and sixth epibranchial placodes.

74 (*A. melas*, 113 hours) is taken through the attachment of the general communis X to the sixth epibranchial placode.

75 to 78 illustrate the formation of the jugular ganglion of the Xth. Fig. 75 (*A. melas*, 69 hours) shows the slight condensation of cells in the future position of the jugular ganglion before the appearance of the root of the X.

76 (*A. melas*, 81 hours). The cells which later form the jugular ganglion inclose the fibrous root of the X.

77 (*A. melas*, 113 hours) shows the first decided increase in size of the jugular ganglion when it begins to mass itself into definite areas of cells such as appear in fig. 78 (138 hours) where the ganglion is broken into small masses by the fibrillated root of the X.



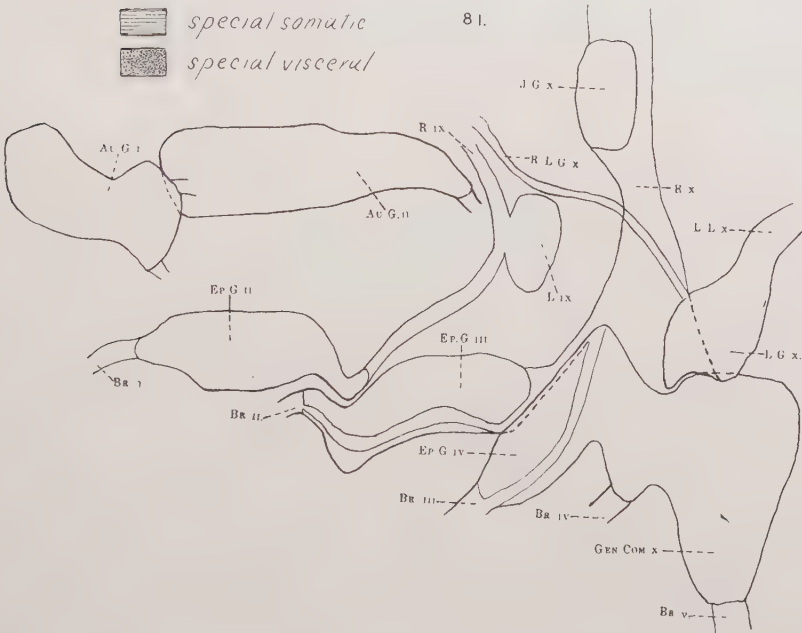
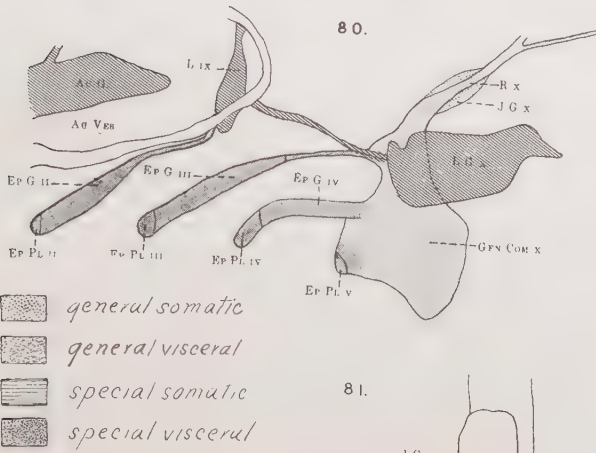
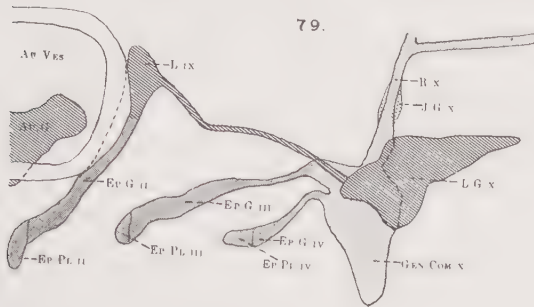
EXPLANATION OF FIGURES

79 to 83 are reconstructions of the cranial ganglia of *A. melas* and are true in two dimensions, the anterior-posterior and the dorso-ventral. The reconstructions were made by projecting the section of the ganglion on paper to determine the vertical length of a given section. The lens of the eye, which is an almost perfect circle in these diameters, was used as a basis for determining the ratio of longitudinal to vertical dimensions. The reconstructions give an approximately exact picture of the lateral view of the ganglia as seen on a flat surface. The figures give no idea of the relative thickness of the ganglia and many of the roots appear as large as the ganglia while in reality they are quite thin, sometimes not more than one cell thick, cf. the roots of the II, III and IV epibranchial ganglia, figs. 79, 80 and 81. The object in making these reconstructions was to trace the embryonic ganglia up to a stage where they could be positively identified as the definitive ganglia of the adult.

79 is a reconstruction of the ninth and tenth ganglia of *A. melas*, 81 hours; only three epibranchial placodes are present at this stage.

80 is a reconstruction of the ninth and tenth ganglia of *A. melas*, 93 hours. Four epibranchial placodes are here present.

81 is a reconstruction of the eighth, ninth and tenth ganglia of *A. melas* 138 hours. All placodes have disappeared some hours previous to this stage.



EXPLANATION OF FIGURES

82 is a reconstruction of the eighth, ninth and tenth ganglia of *A. melas*, 174 hours.

83 is a reconstruction of the fifth, seventh and anterior portion of the eighth ganglia of *A. melas*, 86 hours. The roots of the V and VII ganglia are slightly schematized beyond their origin from the ganglia for the sake of clearness.



83.

